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SEXUAL BEHAVIOUR AND
SEXUAL SELECTION IN NEWTS

A Thesis
submitted for the degree of
Doctor of Philosophy

of
The Open University

by

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ABSTRACT

This thesis reports an investigation of the influence of sexual selection on the sexual behaviour of the European smooth newt, *Triturus vulgaris*, and of the North American red-spotted newt, *Notophthalmus viridescens*. Both belong to the family Salamandridae of the amphibian order Urodela.

Chapter 1 introduces the concept of sexual selection, and those aspects of competition and mate choice relevant to newt sexual behaviour are discussed.

In Chapter 2, observations and experiments are described which demonstrate intermale competition and mate choice in the smooth newt. Males interfere with one another's attempts to inseminate females, a form of competition known as sexual interference. Under certain conditions, males choose larger, more fecund females as mates, whereas females seem to prefer males reasonably well matched to themselves in body length. The extent to which females mate repeatedly is investigated.

In Chapter 3, the sexual behaviour of the red-spotted newt in encounters between single males and females is described. Males adopt one of two types of courtship, depending on the initial responsiveness of the female partner. Using a form of sequence analysis, the male's behaviour is described, and aspects of it are interpreted in causal and functional terms. Data on the various costs and benefits associated with each type of courtship are presented.

Chapter 4 investigates the influence of sexual selection on the behaviour of the red-spotted newt. The male is sensitive to the ambient

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sex ratio in his vicinity, and this ratio influences which type of courtship he undertakes. In competitive situations, males interfere with one another, sometimes in a manner similar to that observed in the smooth newt. In laboratory experiments, it is shown that males prefer larger, more fecund females as mates, and that females will mate with more than one male.

Chapter 5 adopts a comparative approach. The results presented in this thesis are discussed in the context of other urodele amphibians and other animals with similarly complex sexual behaviour. The various types of sexual behaviour in both species of newt are considered as alternative mating strategies, and an attempt is made to classify them in terms of contemporary ideas concerning behavioural strategies.

References are listed in Chapter 6.

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CHAPTER 1

INTRODUCTION

CHAPTER 1

INTRODUCTION

1.1 Sexual Selection - Competition and Choice

Darwin (1871) formulated the theory of sexual selection in order to account for the evolution of morphological and behavioural characteristics which confer an advantage on certain individuals of one sex, usually the male, over others, solely in relation to the acquisition of mates. Darwin recognised two different mechanisms by which mates may be acquired. The first, and most obvious, is by direct competition between males for access to females. The second involves indirect competition between males in attracting and stimulating females, the latter then choosing their mates from the pool of males available.

Drawing on the earlier empirical work of Bateman (1948), Trivers (1972) suggested that males tend to be competitive and 'charming' and females coy and choosy as a result of the different ways in which each sex allocates its resources to reproduction. This allocation is partially made up of what Trivers has called 'parental investment', defined as any investment made by the parent in an individual offspring, which increases the probability of that offspring surviving but decreases the parent's ability to invest in other offspring. Whereas females produce relatively few, large gametes, or ova, which are expensive in terms of the resources required to produce them, males produce relatively large numbers of small, cheap sperm (Parker, Baker and Smith 1972; Maynard Smith (1978). As a result,

female parental investment becomes a limited resource for which males compete. Males tend to allocate more of their resources to mating effort rather than parental effort (Low 1978). Females are expected to 'safeguard' their greater parental investment by choosing to mate only with males who will contribute the most to their offspring in terms of 'good genes', paternal care and/or material resources. In summary, females choose and males compete because maternal fitness is limited by the female's ability to accrue resources, whereas paternal fitness is constrained by the male's ability to achieve fertilizations (Bateman 1948). Historical and critical reviews of the theory of sexual selection can be found in Trivers (1972), Halliday (1978, 1983), Borgia (1979), Otte (1979), O'Donald (1980) and Thornhill (1980a).

There are a multitude of ways in which males compete amongst one another for opportunities to fertilize ova; a number of the more common types of male competition are listed in Table 1.1. However, this list does not show the full complexity of male competition. Because males vary in their competitive abilities and their attractiveness to females, mating success has a higher variance in males than in females (Bateman 1948; Wade and Arnold 1980). For poorly competitive and/or unattractive males, at least a few matings may be obtained by the adoption of an alternative mating strategy, that is, a pattern of behaviour that differs from the behaviour characteristic of the species.

The origins and maintenance of alternative strategies of competition for limited resources are reviewed in Cade (1980), Dawkins (1980), Dunbar (1982), Rubenstein (1980) and Davies (1982). One common alternative male mating strategy is to 'parasitize' another strategy; such 'parasitic' males often attempt to fertilize the ova of females which have been competed-for, attracted and stimulated by the efforts of other males in the population. The classification of alternative strategies is an

1. Adaptations that play a role in the acquisition of mates.
 - a. defense of resources required by females, e.g. food, nest sites, etc.
 - b. defense of groups of females, or harems.
 - c. social dominance; dominant males may gain priority of access to females.
2. Adaptations that ensure paternity.
 - a. mate guarding; either before and/or after sperm transfer.
 - b. copulatory plugs, which occlude the genital tract of the female.
 - c. rendering the female unattractive or unresponsive to other males.
3. Adaptations that lower a competitor's fitness.
 - a. direct assault, with possible physical injury.
 - b. nest destruction.
 - c. induced abortion in a female carrying a competitor's offspring.
 - d. infanticide of a competitor's offspring.
 - e. sperm competition.
4. The adoption of alternative mating strategies in poorly competitive and unattractive males especially.

TABLE 1.1 Major types of male competition in animals
(Modified from Wilson 1975).

unsettled issue (Maynard Smith 1982), but in general, several major categories have been recognised (see Davies 1982):

1. pure strategy; individuals are genetically predisposed to adopt only one strategy (e.g. either A or B).
2. mixed strategy; individuals adopt more than one strategy according to some fixed probability rule (e.g. play A with probability p, B with probability (1 - p)).
3. conditional strategy; individuals are genetically capable of following any alternative, but are limited in their behaviour by some variable such as size, age, population density or the strategies adopted by other individuals (e.g. if x, play A, but if y, play B). This is probably the commonest type of alternative strategy.

Mate choice may be operationally defined as any behaviour which leads to members of one sex being more likely to mate with certain members of the opposite sex than with others (Halliday 1978, 1983). Although parental investment theory has generally predicted that females will be the choosier sex, males may exercise mate choice (Halliday 1983). The criteria and benefits of mate choice are very varied and include choice for:

1. high fecundity or fertility.
2. parental competence.
3. material resources.
4. mate 'complementarity'.
5. effective courtship displays.
6. mate fitness, or 'quality'.

Although it is heuristically useful to consider competition and choice separately, they occur concurrently in the mating systems of many species (Emlen and Oring 1977; Halliday 1983). As discussed more fully later in this thesis, each may have either a facilitatory or an inhibitory effect on the other.

1.2 Amphibians with tails

This brief account is taken from Goin, Goin and Zug (1978). The tailed amphibians, or the order Urodela, comprise the salamanders and newts, a diverse group of about 310 species which range geographically from the Americas to Eurasia. In all but the cryptobranchoid salamanders (the hynobiids and cryptobranchids), fertilization is internal and sperm transfer is accomplished by means of a spermatophore. Although oviparity is the most common reproductive mode, ovoviviparous and viviparous species are also known. Although all of the newts are aquatic at least during the breeding season, the salamanders include aquatic and terrestrial species, the latter restricted to moist microhabitats.

There are seven families in the order Urodela, although only three, the Ambystomatidae, Plethodontidae and Salamandridae (which form part of the suborder Salamandroidea), are of direct concern to the work presented in this thesis.

The Ambystomatidae are salamanders which return to water to breed, but live on land for most of their adult lives. Most species are oviparous, and all are restricted to North America.

The lungless plethodontid salamanders are more or less restricted to the Americas, although one genus is also found in southern Europe. This family is the most successful group of extant urodeles and includes

terrestrial (arboreal and fossorial) and aquatic species.

The salamandrid urodeles are the 'typical' salamanders and newts, and are found in all parts of the urodele range. Salamanders in this family are typically terrestrial, whereas the newts are more aquatic in their habits, especially during the breeding season.

The sexual behaviour of the urodeles has received casual attention for many years, but it is only recently that detailed studies have been made of this topic (e.g. Salthe 1967; Arnold 1977; Halliday 1977a). Most of these studies have looked at the sexual behaviour of single male-female pairs in the laboratory. However, Arnold (1976) made detailed observations of interactions between individuals in more complex social groups, and suggested that intermale competition has influenced the evolution of the sexual behaviour of ambystomatid and plethodontid salamanders. Halliday (1977a) discussed the evidence for mate choice in newts of the genus *Triturus*, but such evidence is indirect and it is clear that further empirical investigation of the nature and effects of mate choice is needed.

1.3 The Aims of the Present Study

The experiments and observations reported in this thesis represent part of a continuing quantitative study of male competition and mate choice in newts in the laboratory. In these respects, they extend Arnold's (1976) observations of competition to another urodele family, the Salamandridae, and extend Halliday's (1977a) work on mate choice in European newts (*Triturus*).

Two species were selected for investigation. The first was the smooth newt, *Triturus vulgaris vulgaris* (Linnaeus), the most common newt

species in Britain and one whose sexual behaviour is already documented in considerable detail (see Halliday 1977a for a review). The second was the red-spotted newt, *Notophthalmus viridescens viridescens* (Rafinesque), one of the two North American newt genera, and one whose sexual behaviour has been fully described (Arnold 1972). Arnold's account does not, however, go into the kind of quantitative detail of Halliday's studies of *Triturus vulgaris*.

CHAPTER 2

SEXUAL SELECTION IN THE SMOOTH NEWT,
TRITURUS VULGARIS

CHAPTER 2

SEXUAL SELECTION IN THE SMOOTH NEWT, TRITURUS VULGARIS

In this Chapter, I review the literature on the natural history (Chapter 2.1) and sexual behaviour (2.2) of the smooth newt, and present experimental evidence (2.4-2.7) which suggests that the sexual behaviour of this species has, at least partially, been influenced by sexual selection during its evolution. The experiments reported here arose from an attempt to detect female mate choice in these newts. It soon became apparent that when a female and two males are placed together, interactions between the males are the most frequent and important that occur.

These interactions closely resemble those described by Arnold (1970) for three salamander species *Ambystoma maculatum*, *A. tigrinum* and *Plethodon jordani*. He has interpreted these as a type of male-male competition known as sexual interference, in which males interfere with one another's attempts to inseminate females. In Chapter 2.4.1, I describe the nature of sexual interference in the smooth newt and in Chapter 2.4.2, the responses of females to it.

Arnold (1976) has also found a number of male behaviour patterns which apparently function as defense against sexual interference. The experiment reported in Chapter 2.5 was designed to investigate such sexual defense in the smooth newt.

Sperm competition, in which the sperm from two or more males compete for the fertilization of a female's ova, is another expression of intra-sexual competition. (Parker 1970; Halliday and Verrell 1983). Sperm competition is only possible if a female mates with more than one male and in Chapter 2.6, I describe an experiment which investigated the extent of multiple mating in female smooth newts.

Both male and female smooth newts may exercise mate choice, choosing mates on the basis of behavioural and/or morphological criteria. In Chapter 2.7, I present data which suggest that both sexes choose partners of certain body sizes.

2.1 The Natural History of the Smooth Newt

The salamandrid genus *Triturus* is widely distributed throughout Europe, part of Scandinavia and part of Asia (Arnold and Burton 1978). Lantz (1947) has divided the genus into three groups of related species, one of which is clustered around the smooth newt, *Triturus vulgaris*. This species is the widest ranging of all of the European urodeles, and is also the commonest in most parts of its range. Nine subspecies have been recognized, of which only one, *T. vulgaris vulgaris*, is found in Britain. Two other congeneric newts are found in Britain, the crested or warty newt (*T. cristatus*) and the palmate newt (*T. helveticus*); both are rarer than the smooth newt in lowland areas (Beebee 1981a).

The natural history of the smooth newt has been described in varying detail by Smith (1951), Steward (1969), Halliday (1972) and Bell (1973), and thus only a brief account with some additional information is given here. Like many other temperate-zone amphibians, the smooth newt divides its time between life on land and in water, with up to nine months of the year spent living a terrestrial existence. On land, the newt tends to be nocturnal in its habits; by day it can be found under rocks and logs, but at night it becomes more active, searching for invertebrate prey. In general, activity is dependent on prevailing climatic conditions, being maximal when it is mild and damp. During the cold winter months, the newt is said to hibernate, but as this cannot be analogous to the true hibernation that occurs in homoiothermic animals, it is probably better regarded as torpidity.

The main breeding season begins in the spring, March-April, when the newt migrates to its breeding pond. At the beginning of the season, the newt becomes readapted for its temporary life in water. Halliday (1972) has discussed these readaptations in detail; they include modification of the tail for swimming, modification of the jaws to enable prey to be

sucked into the mouth, changes in the skin which enable it to act as an accessory respiratory surface, changes in retinal pigmentation, modification of the nares and the recrudescence of the neuromast lateral-line system.

In addition, the male develops his secondary sexual characteristics. The body of both sexes is green-brown in colour, paling to an orange-yellow on the belly. This belly colouration may be aposematic in function (Beebee 1981b). The skin is speckled with dark flecks in both sexes, although that of the male also bears larger, darker spots. A dorsal crest begins just behind the head of the male and extends backwards as a vertical extension of his tail. The female lacks a dorsal crest. Along the lower margin of the male's tail are parallel bright red and blue stripes, which are rendered conspicuous by the display of the male (Verrell 1982a). The male also develops fringes of skin along the digits of his hindlimbs. Darwin (1871) suggested that these aid the male in the pursuit of females by increasing his swimming speed. Beebee (1981b) believes that the fringes act as stabilizers during descent after breathing. Halliday and Joly (1981) suggest that such stabilization is also important during the sudden movements associated with feeding and courtship. The male's cloaca is larger and more rounded than that of the female and contains glands associated with spermatophore production (Noble 1931). The skin of both sexes is highly glandular, but no specialized areas of glandular tissue have been described; specialized areas of glandular tissue are present in many urodele species (Arnold and Houck 1982).

Adult smooth newts tend to be philopatric, returning to the same breeding site in successive seasons (Steward 1969). Males arrive at the site before females and migration only occurs under suitable conditions of humidity and temperature (Harrison, Gittins and Slater 1983). The annual survival rate of adults has been estimated at about 50 per cent (Bell 1977).

and adult sex ratios vary from an excess of males (Hagstrom 1979) to an excess of females (Bell 1977). Cooke and Frazer (1976) have surveyed ponds in central England in order to determine the habitat requirements of smooth newts. In general, they prefer slightly alkaline, calcium-rich water, and may assess the suitability of a pond on the basis of its aquatic vegetation, especially algae. Beebee (1981a) has found that scrub or woody vegetation in the nearby terrestrial habitat is also an important correlate of the presence of smooth newts in a body of water.

In the breeding pond, males appear to move around more freely than females, although Dolmen (1981) has suggested that males may maintain home ranges (this has also been suggested for the crested newt by Gauss 1961). Males seem to show a dual rhythm of activity, with sexual behaviour most frequent at dawn and, especially, dusk (Dolmen 1976; R. Griffiths, unpublished data).

Oviposition begins between three and ten days after insemination, and takes place at night (Dolmen 1976). The female wraps each egg singly in the curled leaf of a water plant and there is no subsequent parental care. Bell (1977) suggests that whereas males are probably ready to breed as soon as they enter the water, females require some time in the water before they have matured their full complement of oocytes for the season. Bell, studying a population near Oxford in England, also found a positive correlation between female age (and size) and the total number of yolked oocytes in the ovary, which represents the number available for fertilization. However, Hagstrom (1980a) has failed to find a similar correlation in newts from a population in Sweden.

The eggs of the smooth newt hatch after about 21 days, giving rise to tiny, wholly carnivorous tadpole larvae. Bell and Lawton (1975) estimated the mean survival of hatchlings as about 2.5 per cent. They

also detected three cohorts of larvae in their Oxford population. The earliest consisted of larvae from the previous year. Larvae produced by the spring migrants comprised the main cohort, which also enjoyed the highest survivorship. Larvae produced in the autumn by animals making their first breeding effort formed the late cohort; some of these overwintered in the water and formed the early cohort of the next year. Recent work conducted in the Milton Keynes area of south-east England has failed to reveal any evidence for an autumnal migration (A. Bielinski, unpublished data).

After metamorphosis, the juvenile newt leaves the water and begins its residence on land; it remains a terrestrial juvenile until it attains sexual maturity. Bell (1977) estimated the survival of such juveniles as about 80 per cent, with maturity reached between the ages of three and seven years. (Bell estimated the age of his animals by statistically transforming data on body length. More reliable aging techniques have since been developed, e.g. the counting of growth annuli in bone; Hemelaar and van Gelder (1980). Males seen to attain sexual maturity before females; the latter may defer maturity in order to divert their resources to greater somatic growth (as suggested above, female fecundity is size-related). Most adults leave the water at the end of the breeding season in June-July, although some overwinter in the water.

Predation on smooth newts is greatest during the aquatic stages of the life cycle, especially for eggs and larvae. Predators include birds, snakes, water-beetles, leeches and crested newts (Hagstrom 1971, 1979). Adult smooth newts will readily cannibalise their own larvae if kept in captivity. Fishes are major predators, and ponds containing large numbers of fish tend to support only small populations of newts (Beebee 1981a).

2.2 The Sexual Behaviour of the Smooth Newt

Our understanding of the sexual behaviour of the smooth newt is due primarily to the efforts of T.R. Halliday. His extensive research into this topic has been recently reviewed (Halliday 1977a, 1980) and thus only a brief survey of the literature is given below.

A sexual encounter between a male and a female consists of a variable number of sequences, each terminating in the deposition of a spermatophore which the female may or may not pick-up with her cloaca. Each sequence can be divided into a number of discrete phases which tend to occur in a reasonably well-defined order (see Halliday 1974 and Figure 2.1). The

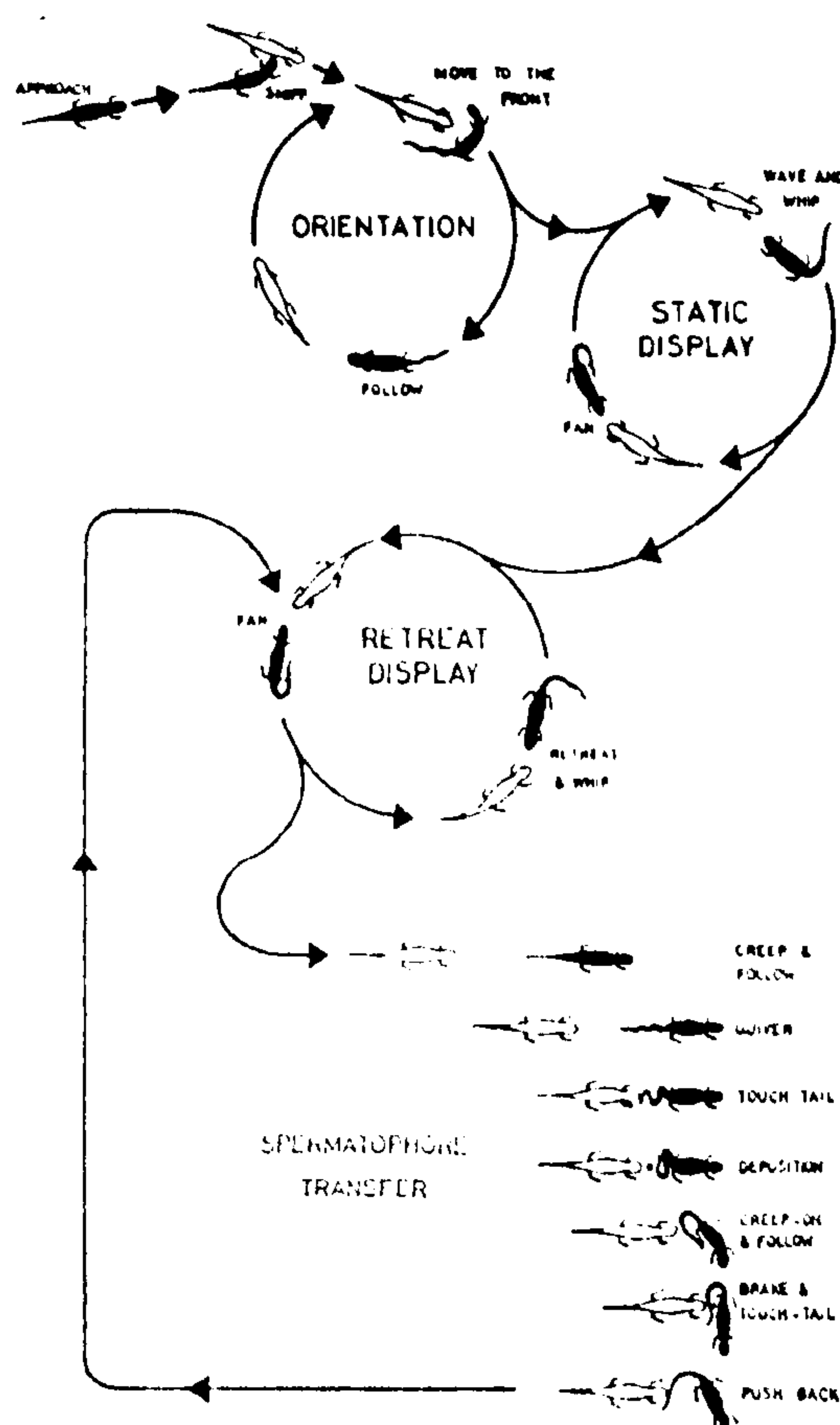


Figure 2.1 Diagrammatic summary of the sexual behaviour sequence in the smooth newt. The male is in black. Taken from Halliday (1974).

first sequence of an encounter begins with an orientation phase in which the male repeatedly attempts to take up a position in front of the female, using an action referred to as 'move to the front'. When in front of his partner, the male begins to display with three distinct movements of his tail, known as 'wave', 'whip' and 'fan'. These stimulate the female with visual, mechanical and olfactory cues, respectively (Halliday 1975a, Verrell 1982a). The female remains more or less stationary during this phase, which is known as static display.

After a while, the female begins to approach the male, who moves backwards, away from her. During this phase, called retreat display, the male continues to display to the female using his tail, mainly with waves and whips. Provided the female responds positively to the male by continuing to approach him, he will turn away from her and initiate spermatophore transfer behaviour (Halliday 1975b).

When fully turned away, the male 'creeps' ahead of the female with a jerky, shuffling movement. He then 'quivers' his tail laterally. The female follows and literally bumps into his quivering tail with her snout. This 'tail touch' to the male is the stimulus that elicits the deposition of a spermatophore from him (Halliday 1975b). The male then moves forwards a little more ('creep-on'), turning through an angle of 90° , and stops ('brake'), blocking the female's path. In moving forwards, the male leaves a distance of about one snout-vent body length between himself and his spermatophore. Provided the female follows the male closely during creep-on, she should be positioned with her cloaca in the close vicinity of the spermatophore, which may be picked up. When in the brake position, the male may push the female backwards by flexing his tail ('push-back').

If the female remains close to the male at the end of the first sequence, he may initiate a second, which, because the female is still responsive,

begins with retreat display; the orientation and static display phases generally only occur in the first sequence of an encounter. Up to six sequences may comprise a single encounter, although between two and four is more usual. Halliday (1974) found that 61 per cent of encounters result in the insemination of the female by at least one spermatophore, and that the probability of a spermatophore being picked up is greater for those deposited in the later sequences of an encounter (see Figure 2.2).

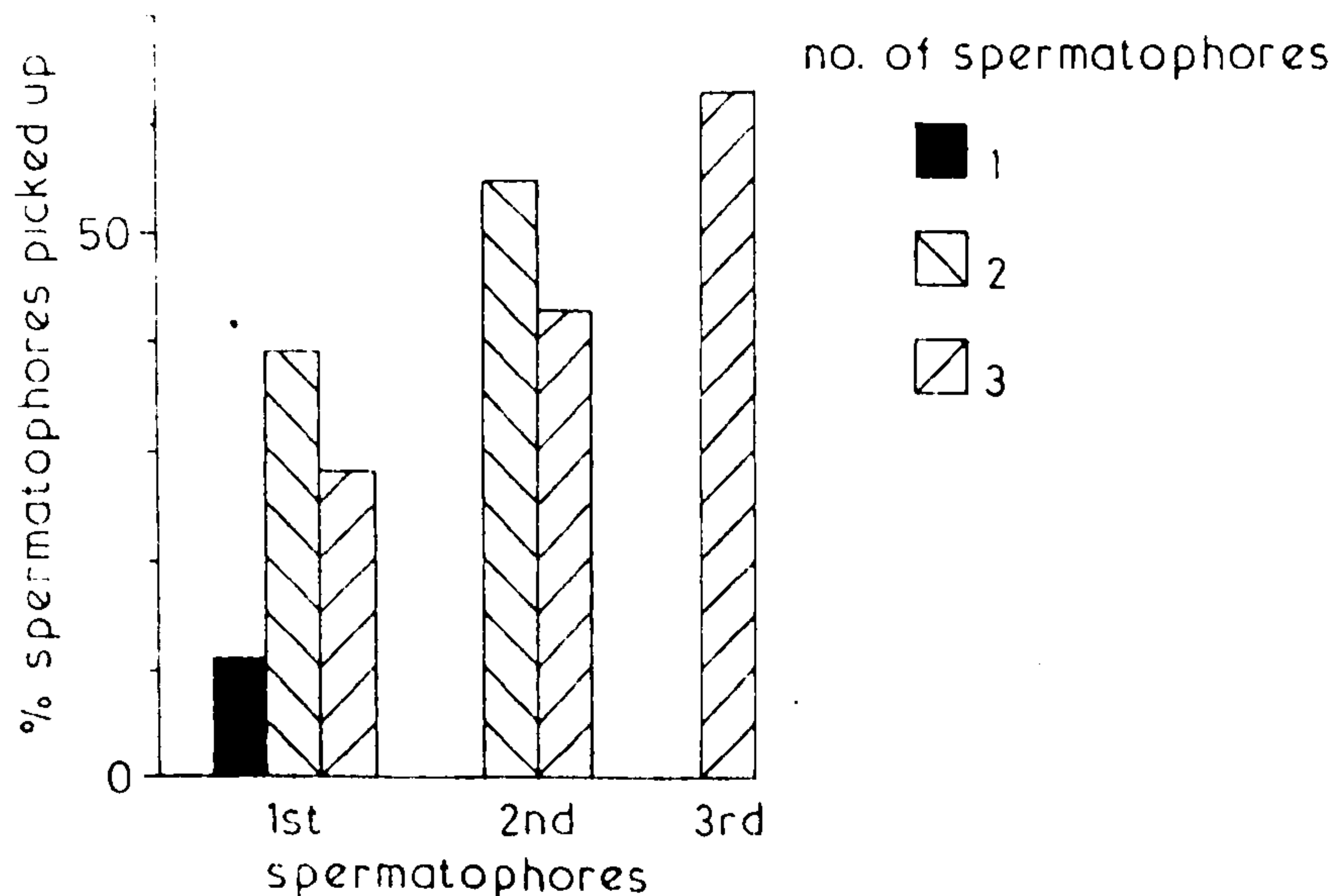


Figure 2.2 Sequence success in the smooth newt. As the probability of spermatophore pick up increases as more sequences of courtship are completed, females may be selectively inseminated by males able to deposit large numbers of spermatophores. Taken from Halliday (1974).

A number of the male's actions during courtship are positively correlated with the number of spermatophores he subsequently deposits, for example, the total duration of fanning during static display (Halliday and Houston 1978). Males with many spermatophores to deposit court rapidly, but those with fewer court more slowly and tend to vacillate between retreat display and the initial stages of spermatophore transfer behaviour. These differences in the sequential patterning and timing of the male's display behaviour, correlated with spermatophore supply, have

been transformed by principal components analysis into a single variable, labelled 'libido' (Halliday 1976). Changes in libido can be observed for a single male over successive sequences within a single encounter and over successive encounters (Halliday 1976).

One major problem for a male newt concerns his need for oxygen for, under non-sexual conditions, breathing rate and activity are positively correlated (Halliday and Worsnop 1977). When faced with the choice of either postponing breathing or leaving the female in order to breath, Halliday and Sweatman (1976) found that the courting male only interrupts his courtship early in a sequence or at its very end; the critical phase of spermatophore transfer behaviour is never interrupted. The availability of oxygen also influences the timing of the male's behaviour, it being more rapid when oxygen is scarce (Halliday 1977b). Thus spermatophore supply and oxygen availability are two important internal factors which influence the male's courtship behaviour. The responsiveness of the female is an important external factor in this respect (Halliday 1975b). These causal factors have been incorporated into a computer model of smooth newt courtship which simulates observed behaviour quite accurately (Houston, Halliday and McFarland 1977; McFarland 1977).

In the tradition of a 'classical ethologist' (c.f.: Tinbergen 1963), Halliday has also considered aspects of the evolution and function of newt sexual behaviour. As discussed in detail in Halliday (1972, 1977a), the behaviour of all of the species in the genus *Triturus* is similar in general form and can be used to construct a putative phylogeny of the genus and of the family Salamandridae, the latter of which agrees reasonably well with phylogenies based on other diagnostic characters, such as the phylogeny based on morphological characters proposed by Wake and Ozeti (1969). Some of the differences between the species in the genus may be of significance in the maintenance of premating reproductive

isolation, for example fanning speeds in *T. vulgaris* and *T. helveticus*, which are highest in the latter species (see also van Gelder 1979).

The sexual behaviour of the newt may have another function besides facilitating the insemination of conspecific females, that being the assessment of the 'quality' of potential mates. Mate choice may be defined as any pattern of behaviour that leads to members of one sex being more likely to mate with certain members of the opposite sex than with others (Halliday 1983). The following have been suggested by Halliday (1977a) as being relevant to mate choice in the smooth newt.

1. Mate choice in the female:

- a. because the probability of pick up is greater for spermatophores deposited later in an encounter (Halliday 1974), females may be more likely to be inseminated by males able to produce large numbers of spermatophores.
- b. the male 'advertises' the number of spermatophores he is able to produce in his static display (Halliday and Houston 1978). This may enable females to assess the fecundity of the male early in an encounter.
- c. the secondary sexual characteristics of the breeding male (described in Halliday 1975a) suggest the influence of sexual selection in much the same way as do the epigamic characteristics of peafowl (Darwin 1871).
- d. females might mate preferentially with males of a particular size (Halliday 1977a), especially if male fecundity is size dependent or size is a reliable indicator of male 'quality', e.g. ability to survive and accrue resources necessary for growth.

2. Mate choice in the male:

- a. males might preferentially mate with females of a particular size, especially if female fecundity is size dependent (Halliday 1977a).
- b. males vacillate more frequently between retreat display and spermatophore transfer behaviour in the later sequences of an encounter (Halliday 1976). Because the probability of spermatophore pick up is greater in these sequences, vacillation may be a means of ensuring that the female is 'committed' to continuing the encounter (Halliday 1977a).

It is quite clear that the two components of sexual selection, competition and choice, can occur simultaneously within single sexual encounters in many species (reviewed by Halliday 1983). The work reported in this Chapter was undertaken to investigate the nature of sexual selection in the smooth newt.

2.3 General Methods

Origins of Animals

The smooth newts used in all of the experiments described here were collected from populations in the Oxford and Milton Keynes areas of southern England. The majority of animals were collected in their aquatic phase during the breeding season either by dip-netting or by capture in modified minnow-traps. In addition, some individuals were collected as they migrated to their breeding ponds at the start of the breeding season. A number of animals in this latter group were captured in pit-fall traps placed around ponds.

After use, the newts were returned to their site of origin, except for a small number of newts from Oxford which were sacrificed and preserved.

Keeping of Animals

All animals were maintained in storage aquaria measuring 122 x 38 x 38 cm; individuals were segregated with respect to both sex and site of origin, with no more than 20 animals per aquarium.

The storage aquaria were floored with a mixture of pea gravel and silver sand, and contained a few large stones. Various aquatic plants were added when available. The tanks were encouraged to develop as rich an invertebrate fauna as possible; each contained a few planorbid snails in order to check algal growth. The newts were given a liberal diet of live food items including *Daphnia*, *Tubifex*, insect larvae and chopped-up earthworms. The water in the tanks was neither aerated nor filtered, and its temperature fluctuated about 2°C around 10°C. A photoperiod schedule of 16h light, 8h dark (lights on at 0600 hours) was observed, to mimic spring. For animals kept in 1980 and 1981, illumination was provided by ordinary fluorescent light tubes, but in 1982, these were replaced by Truelite tubes, which produce the same mix of wavelengths found in natural sunlight.

Experimental Procedure

All experiments were conducted in one of two observation aquaria. These measured 61 x 30 x 30 cm and were floored with fine silver sand. Water weeds were not planted in these tanks, but the water was aerated and filtered. The temperature of the water varied between 18-22°C.

Both observation tanks were surrounded with a scaffolding framework to which was attached a video camera. Most experiments were recorded

as an audiovisual commentary using a videotape recording system with simultaneous audio input (National Panasonic VTR-NV-8030). These commentaries were subsequently transcribed from the videotape records onto paper.

In general, each individual newt was used as seldom as possible, thus ensuring that all statistical tests were conducted on independent data. Where necessary, individual newts were recognized by recording patterns of spots on the throat and belly, a technique modified from Hagstrom (1973).

Details of specific procedures and techniques used are given in the 'Methods' and 'Results' sections of individual experiments.

2.4 Sexual Interference in the Smooth Newt

The experiments reported here were designed initially to demonstrate female mate choice in triads consisting of one female and two males. However, during pilot experiments, it soon became apparent that the most frequent interactions observed were between the two males, with little or no evidence for female mate choice. These male-male interactions closely resembled those described by Arnold (1972, 1976, 1977) for the salamanders *Ambystoma tigrinum*, *A. maculatum* and *Plethodon jordani*. Arnold interpreted these as a type of intrasexual competition known as sexual interference, in which males interfere with one another's attempts to inseminate females. This section provides a quantitative analysis of sexual interference in the smooth newt.

2.4.1 The Nature of Sexual Interference

Method

A female was placed in an observation tank and allowed 10 minutes to settle. Two males of equal length were then placed with the female, and all interactions between individuals in the resulting triad recorded as an audiovisual commentary on videotape. A maximum period of observation of one hour was allowed for each triad, and a total of 78 such encounters were observed in which the female responded to one of the two males. All triads involved different individuals.

In addition, 20 encounters between a female and a single male (a dyad) were observed, again involving different animals. These encounters proceeded much as described in Chapter 2.2 and Halliday (1974). The data derived from them were used in quantitative comparisons with the triads.

Results

Of the 78 triadic encounters observed, male-male interactions occurred in 45 (59 per cent). The other 33 encounters proceeded in a manner similar to the dyads observed, and are excluded from further consideration unless otherwise stated.

In a typical encounter involving interactions between the males (41 out of the 45), one male, hereafter called the 'courter', would begin to display to the female. He would proceed through the courtship sequence to creep, the action which initiates spermatophore transfer behaviour. At this point, the other male, hereafter called the 'rival', would approach the courting pair and move between the partners. In this position, the rival would mimic the behaviour normally shown by the female at this time, and nudge the tail of the courter with his snout. In this

way, the rival would elicit the deposition of a spermatophore from the courter, who would then enter the highly stereotyped stage of post-deposition behaviour (creep-on and brake). This would leave the female closer to the rival male, who would then creep himself, in effect 'inviting' the female to initiate spermatophore transfer behaviour with him. This type of sexual interference by female mimicry is depicted in Figure 2.3.

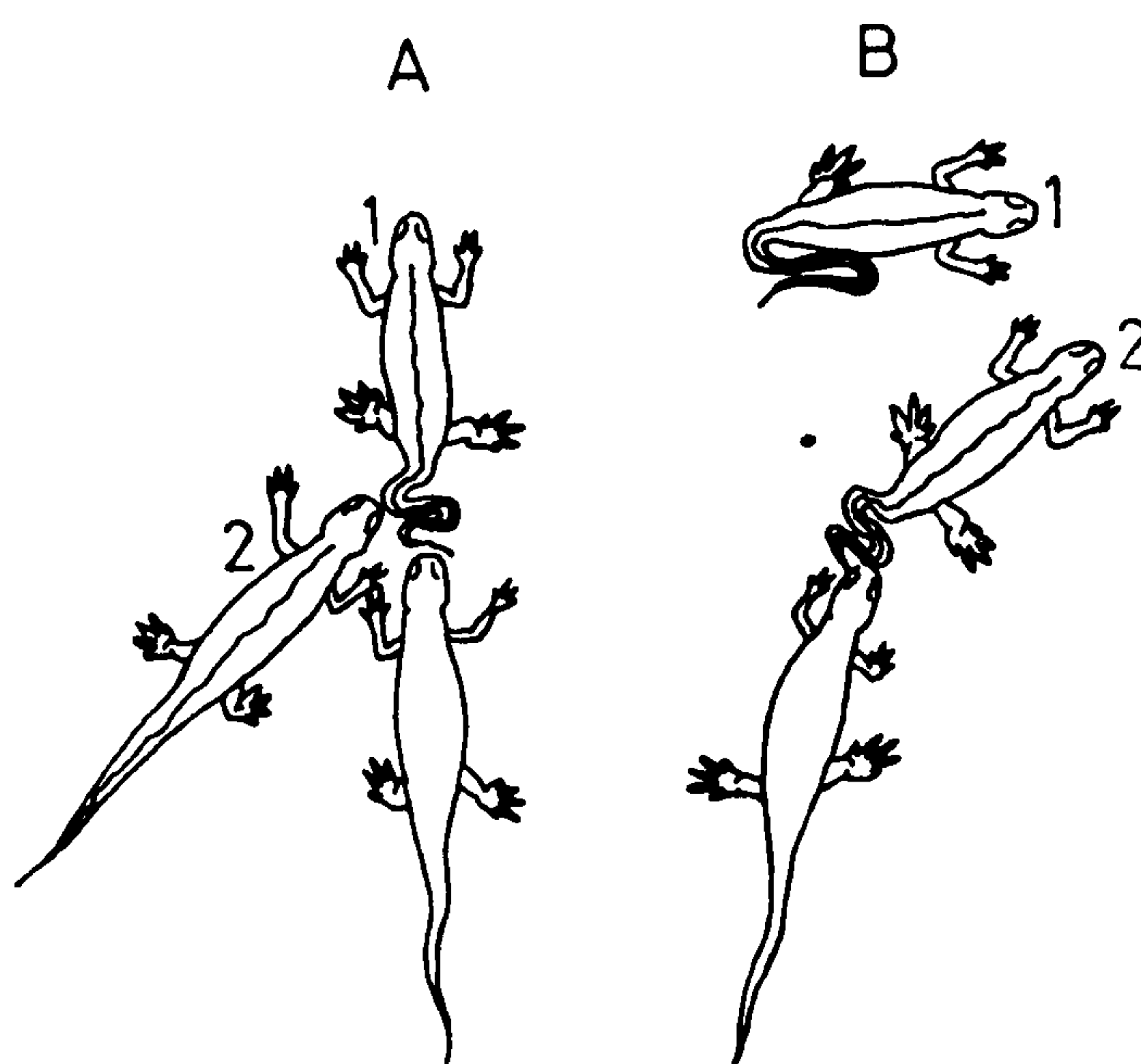


Figure 2.3 Sexual interference in the smooth newt. A: as male 1 creeps, male 2 touches his tail and elicits the deposition of a spermatophore. B: male 2 then creeps, followed by the female, as male 1 assumes the brake position.

Other types of male-male and rival male-female interactions were also observed, some occurring before and some instead of female mimicry. For instance, the rival would sometimes display to either the courter or the female, which resulted in one of these two leaving the other. However, female mimicry was the most frequent type of interaction observed.

Using this strategy of sexual interference, the rival male alone inseminated the female in seven of the 45 encounters observed. In a further

two, the female picked up sperm first from the courter and then from the rival, i.e. was multiply inseminated as a result of sexual interference. Table 2.1 shows that the probability of the courter transferring at least one spermatophore to the female per courtship encounter was significantly lower in triads involving interference than in dyads. The probability of the female becoming inseminated, by either or both males, was also lower in triads (47 per cent) than in dyads (65 per cent), but this difference was not significant.

| | Female: | |
|--------|-------------|-----------------|
| | Inseminated | Not Inseminated |
| Dyads | 13 | 7 |
| Triads | 12 | 33 |

$$\chi^2 = 8.6, P < 0.001$$

Table 2.1 The probability of the courter transferring at least one spermatophore to the female in dyadic and triadic encounters.

In dyadic encounters, the display of the male is thought to increase the responsiveness of the female (Halliday 1977a). At first, it was felt that in triads the rival male might be exploiting the efforts of the courter in rendering the female responsive. This may benefit the rival in that he would avoid the costs of time, energy and oxygen consumption associated with the often lengthy orientation phase of an encounter. It may also benefit the rival given that the probability of spermatophore pick up increases as more sequences are completed and hence more stimulation is provided to the female (Halliday 1974). One outcome of such exploitation would be that triadic encounters would contain more sequences than are completed in dyads, the rival 'tagging' his courtship onto the end of that of the courter. This prediction is refuted by the data presented in Figure 2.4, in which the probability of an encounter surviving over

successive sequences is plotted for dyads and triads. The mean (\pm SEM) number of sequences per dyad, 2.7 ± 0.6 , was significantly higher than the number per triad, 2.02 ± 0.3 ($Z = 2.47$, $P = 0.02$).

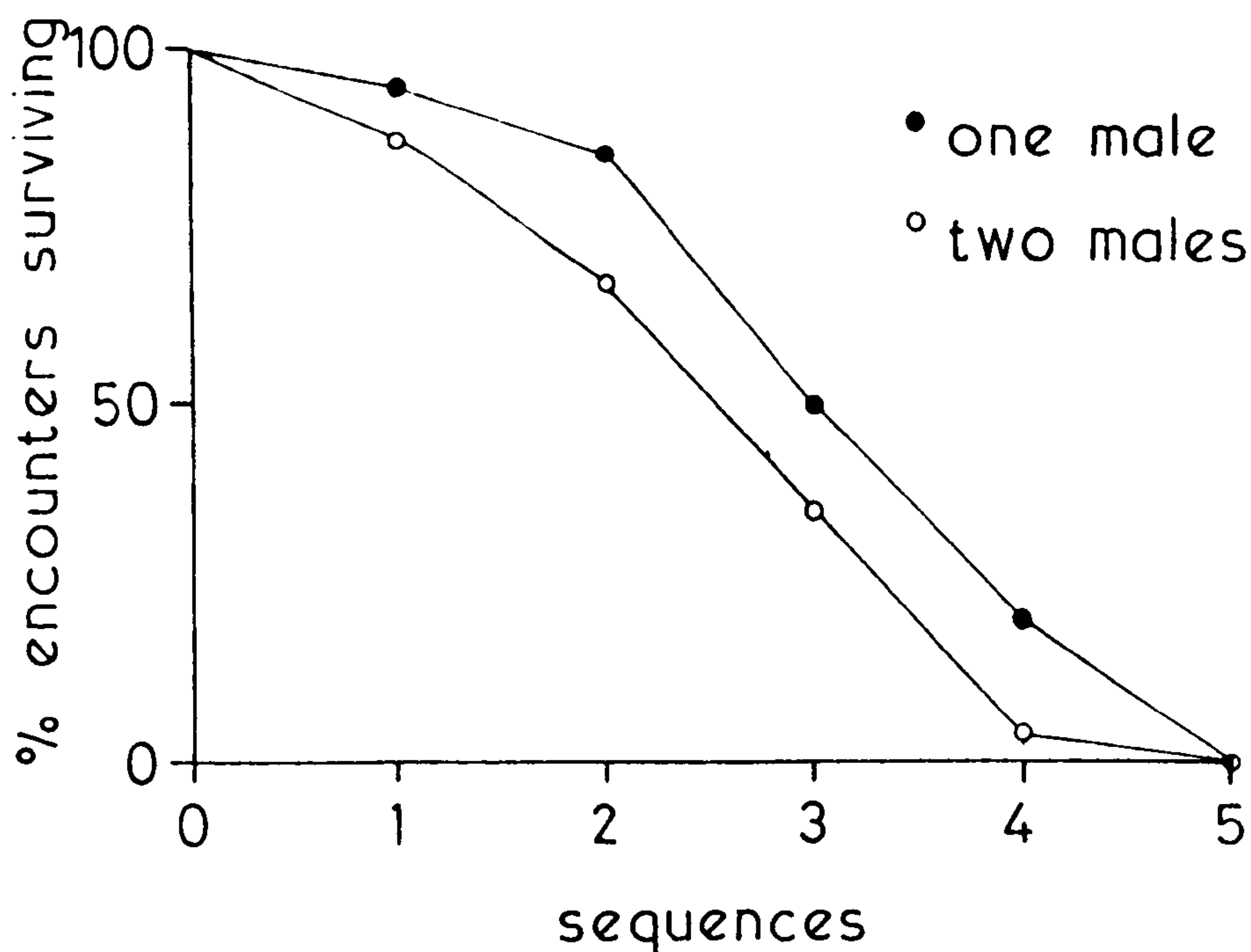


Figure 2.4 The probability of dyadic and triadic encounters surviving over successive sequences.

Coupled with this finding that triadic encounters contain fewer sequences than dyadic ones is the observation that no female was ever observed to elicit more than one spermatophore deposition from a rival; indeed, many fled as soon as the rival interfered. When a female left a competitive situation, she would often ascend to the surface of the water, breath and remain there, more or less motionless.

Thus, females appeared to find encounters involving more than one male 'aversive'. This aversion was most obvious when the rival interfered early in an encounter. As is shown in Table 2.2, the probability that the female would flee as soon as the rival interfered became lower as more sequences were completed with the courter. Not surprisingly, the probability that the female elicited a spermatophore deposition from the rival was greater as more sequences were completed with the courter, and there was

also a slight increase in the probability of the rival's spermatophore being picked up by the female.

| | Number of sequences completed before rival male interferes. | | |
|---------------------------------------|---|-------------|-------------|
| | 1 N = 8 | 2 N = 18 | 3 N = 15 |
| female flees as rival approaches | 6 (75%) | 7 (39%) | 3 (20%) |
| rival deposits a spermatophore | 2 (25%) | 11 (61%) | 12 (80%) |
| female picks up rival's spermatophore | 1 (13%) | 4 (24%) | 4 (27%) |

Table 2.2 The relationship between the success of an interfering rival and the previous behaviour of the courter in triads.

Discussion

When a male smooth newt encounters a female who is already being courted, he will sometimes interfere with the proceedings, attempt to usurp the courting male and perhaps inseminate the female himself. By nudging at the tail of the courter, the rival causes him to deposit a spermatophore and then enter the highly stereotyped behaviour of creep-on and brake. Indeed, this behaviour is so stereotyped that, in dyads, the male will perform it even if the female is taken away from him. It is interesting to note that the courter cannot retaliate against the rival at this time because of this behavioural stereotypy.

By 'stealing' inseminations, the rival is able to increase his short-term mating success. By mimicking female behaviour, he is also able to significantly depress the short-term mating success of the courter. By causing the courter to deposit a profitless spermatophore from an already

limited supply of sperm (see Halliday 1976), the rival may reduce the longer term mating success of the courter, also. Table 2.3 summarizes some of the costs and benefits associated with either courting a female in a conventional manner, or interfering in an ongoing encounter. It must

| | Courter | Interferer |
|-------------------------------------|----------|-------------|
| effort required to stimulate female | Much | Little |
| opportunities for insemination | Several* | One or none |
| depletion of sperm supply | High | Low |
| sperm competition | ? | ? |

*reduced by sexual interference

Table 2.3 Some of the costs and benefits associated with the alternative mating strategies of male smooth newts.

be stressed that a male is capable of acting as both a courter and a rival. The way he behaves at any one time seems to be solely conditional on whether the female he encounters is alone or already engaged in courtship. Although a male invests more time, and, presumably, energy in his sexual behaviour when he courts a female, the gain he receives in terms of insemination is greater than that which accrues to a rival (although the courter's gain is lower if he suffers sexual interference). As a female may be inseminated by both males in a triad, the possibility that their sperm compete for the fertilization of her ova is raised. It is not clear whether either of the two males would be at an advantage in terms of such sperm competition, depending on whether he is the first or last to inseminate the female (for a further discussion of sperm competition, see Chapter 5).

Females apparently find competitive courtship encounters aversive, although they are more likely to remain with a rival if they are first

exposed to the display of a courter. In causal terms, this exposure may so motivate a female that a 'time lag' of one spermatophore deposition is introduced between the rival's approach and the aversion coming into force. The aversion is harder to explain in functional terms. Females may terminate triadic encounters because they suffer a reduced probability of insemination. Of course, the female could improve her chances of being inseminated by remaining with the rival, and so this explanation is not wholly satisfactory. Another possibility is that females terminate competitive encounters because the activities of a rival thwart the females' ability to effectively express specific preferences for their courtiers over other males in the vicinity. Female mate choice is considered in Chapter 2.7.1 but at present, this explanation remains untested. A final functional explanation has been suggested by T.R. Halliday (personal communication) in which the aversion serves as a mechanism for preventing insemination by sexually interfering males of species closely related to *T. vulgaris*. Again, this is an untested hypothesis, but from Halliday's (1977a) own studies of heterospecific courtship, seems possible, as a female will respond to a heterospecific male if she is first courted by a conspecific.

This description of sexual interference in the smooth newt is the first such account in the literature on salamandrid sexual behaviour, and bears some close similarities with the descriptions of Arnold (1972, 1976, 1977) of sexual interference in ambystomatid and plethodontid salamanders. In *Ambystoma tigrinum*, female mimicry enables a rival to place a spermatophore on top of that of another male (Figure 2.5). Only the uppermost spermatophore is available to the female. In *Plethodon jordani*, a rival will supplant a female by mimicking her behaviour, this causing her to flee. Sexual interference in the smooth newt does not involve spermatophore covering; instead, the rival leads the female away from the courter and then attempts to inseminate her. As in *P. jordani*,

females often flee without being inseminated.

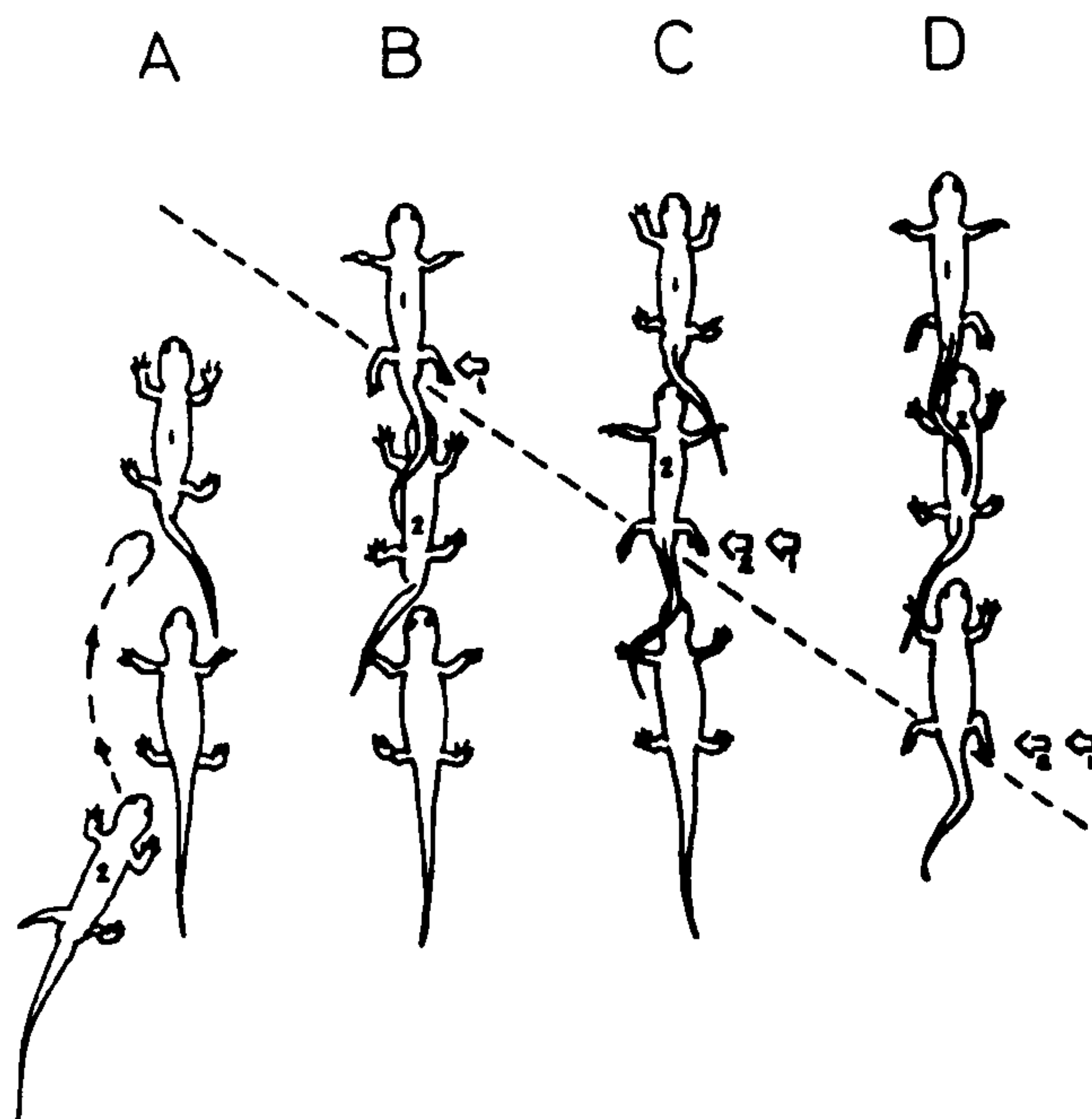


Figure 2.5 Sexual interference in the salamander *Ambystoma tigrinum*.
 A: male 1 initiates spermatophore transfer behaviour with the female. B: male 2 moves between the pair and elicits the deposition of a spermatophore from male 1. C: male 2 then deposits his own spermatophore on top of that of male 1. D: only the uppermost sperm cap, that of male 2, is available to the female. Taken from Arnold (1976).

The results of this experiment posed two further questions concerning intermale competition in the smooth newt. First, how does a courting male respond to a rival? Arnold (1976) suggests that defensive behaviour will co-evolve with sexual interference in the manner of an 'arms race' (*sensu* Dawkins and Krebs 1979). This question is addressed in Chapter 2.5. Secondly, if females find triadic encounters aversive, how do they respond to different densities of males? This question is investigated in the experiments described in Chapter 2.4.2.

2.4.2 Female Responses to Male Density

The behaviour of female newts observed in the last experiment suggested an aversion to the immediate presence of more than one male.

The experiments described in this section were designed to investigate the effect of densities of males in more detail.

Method

In these experiments, proximity was used as an indicator of preference. Such a paradigm has been used extensively in the study of phonoresponsiveness in female anurans (e.g. Gerhardt 1981) and makes the assumption that similar preferences would occur if the animals used were unrestrained.

An observation tank measuring 61 x 30 x 30 cm was wrapped in black cartridge paper to preclude external visual cues and divided lengthways into six sectors of equal size by drawing vertical lines on the paper. Two transparent plastic boxes measuring 20 x 12 x 12 cm were inverted and submerged in the penultimate sectors at each end of the tank. In the first experiment, a single male was placed under one box; the other box contained four males. A female was then released in the centre of the tank, and her position in terms of which of the sectors she was in was recorded at the end of each minute for a period of 30 mins. Ten females were tested in this way. The positions of the one male and four males were then reversed, and a further 10 females tested. The same procedure was followed in the second and third experiments conducted except that in them the choices were between one male and two males and one male and an empty box, respectively.

Results

The results of these experiments are depicted as histograms in Figure 2.6. The data for individual females were extracted from the records for these experiments, and the amount of time spent by each

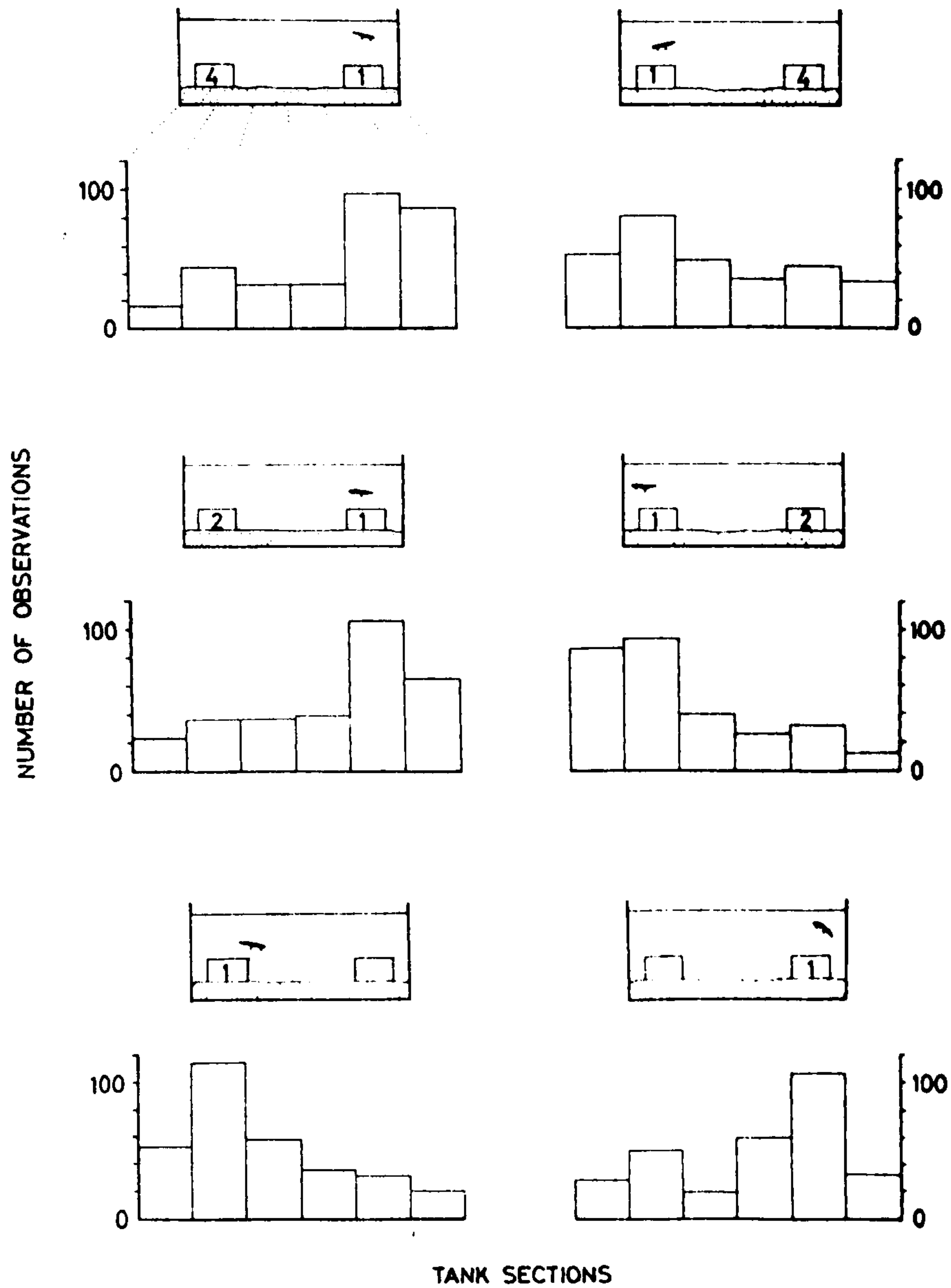


Figure 2.6 Histograms showing the responses of females to different densities of males. Statistical analysis of these data are presented in Table 2.4.

| | |
|-------------------------|-------------------|
| <u>Experiment One</u> | |
| 4 males, 1 male | 1 male, 4 males |
| $P = 0.05$ | $P = 0.011$ |
| <u>Experiment Two</u> | |
| 2 males, 1 male | 1 male, 2 males |
| $P = 0.05$ | $P = 0.001$ |
| <u>Experiment Three</u> | |
| 1 male, empty box | empty box, 1 male |
| $P = 0.001$ | $P = 0.001$ |

Table 2.4 1 x 6 Chi-square tests for the histograms shown in Figure 2.6.

Results of sign-tests conducted on the raw data for individual females which are summarized as histograms in Figure 2.6.

female in the vicinity of each male density was examined with the non-parametric sign-test. The levels of significance derived from these sign-tests are presented in Table 2.4. Females spent significantly more time in the vicinity of one male relative to an empty box, two males and four males.

Discussion

The results of these experiments suggest that females find males visually attractive (experiment three), but only if they are on their own (experiments one and two). In accord with the findings discussed in Chapter 2.4.1, females find groups of males relatively aversive. It is also apparent that these groups of males do not have to be behaving sexually in order to induce this aversive response.

Three possible functional explanations for this aversion were discussed in section 2.4.1. In some animal species, females find aggregations of males attractive, perhaps because such aggregations afford some protection against predation (Hamilton 1971) and/or because they facilitate mate choice, e.g. lek mating systems (Emlen and Oring 1977). Furthermore, in some species females actually 'incite' intrasexual competition, mating with the winners of the ensuing contests, e.g. bison (Lott 1981) and elephant seals (Cox and Le Boeuf 1977).

In causal terms, females might be expected to find aggregations of males more attractive than single males since the former offer a stronger sexual stimulus. Nevertheless, for whatever reasons, females seem to prefer their males 'one at a time'.

2.5 Sexual Defense in the Smooth Newt

As stated in Chapter 2.4.1, males may be expected to evolve defensive mechanisms to counter sexual interference from rivals (Arnold 1976). In the smooth newt, sexual interference by female mimicry can reduce the mating success of a courting male, at least in the short term, and thus the evolution of such sexual defense would be expected to be strongly favoured in this species. However, no evidence of sexual defense was apparent from the observations described in Chapter 2.4.1; indeed, the rival seemed to time his activities such that the courter was unable to retaliate. In this section, I shift attention away from the rival to the courter in order to investigate more fully the behaviour of the latter during competitive courtship encounters.

Method

Halliday (1976) devised a 'standard courtship test', in which the female's behaviour was carefully controlled, in order to examine factors involved in male sexual motivation. The experiment described here is based on a slight modification of Halliday's design, and permits a comparison of the content and timing of a courter's sexual behaviour in the absence and presence of a rival.

A female newt was anaesthetized in a 0.1 per cent aqueous solution of MS 222 and was then placed in a 'strait jacket'. This consists of a length of slit polythene tube, into which the female is inserted, attached at right angles to a rigid perspex rod. When held in this device, the female is transformed into a perfect puppet, whose 'behaviour' is under the control of the experimenter (Halliday 1976).

In order to investigate the effects of a rival on the behaviour of the courter, two types of standard courtship test were conducted:

- (a) Dyadic - with only one male present at any time.
- (b) Triadic - with two males present. The female was made to respond only to one, selected randomly from the two present.

Males were placed in an observation tank and allowed 10 mins. to settle. Those which failed to settle were removed and replaced. A strait-jacketed female was made to approach the courter as he descended from the water surface after breathing. If he responded to the female by displaying with his tail, she was kept more or less stationary for 60 seconds to mimic static display. At the end of this period, the female was made to move towards the male at a constant speed, causing him to initiate retreat display. By responding positively to all of the male's subsequent actions, the female was able to elicit full sexual behaviour from him.

A test was terminated if the male lost interest in the female or consistently fled when approached by her. A test was also terminated if more than 120 seconds elapsed from the last spermatophore deposition with no indication of another being initiated (this criterion was developed by Halliday 1976).

All encounters were recorded as an audiovisual commentary on videotape and the following scores were extracted from the records for each test:

1. the number of bouts of fanning during the 60 second static display period.

2. the total time spent fanning during the 60 second static display period.
3. the number of waves performed during the 60 second static display period.
4. the number of whips performed during the 60 second static display period.
5. the duration of each period of retreat display (defined as the interval from the start of retreat display to the start of the male's last creep before spermatophore deposition).
6. the number of whips performed during each retreat display period.
7. the whip rate (number per 100 seconds) during each retreat display period.,
8. the number of vacillations between retreat display and the initial stages of spermatophore transfer behaviour in each sequence of an encounter.
9. the interval from the start of the last creep before spermatophore deposition in each sequence of an encounter.
10. the interval from the act of deposition to the start of the next retreat display period in each sequence of an encounter.

Only data for encounters of two and three sequences in duration are considered for analysis, all involving different individuals. Because of the relatively large sample sizes from which the data presented here are derived ($N = 30$), the parametric t-test was used to compare scores from dyads and triads (a number of Mann-Whitney u-tests were conducted on parts of these data, which yielded similar significance levels as the t-tests).

Results

1. Static Display. The data for the four scores analyzed for the static display periods are summarized in Table 2.5. The total time spent fanning was significantly greater in triads, although the number of fan bouts was unaffected, i.e. the duration of these bouts was increased. The presence of a rival did not affect the number of waves performed, but the number of whips was lower for triads of three sequences duration.

2. Retreat Display. As Table 2.6 shows, all retreat display periods were of significantly longer duration in the presence of another male. In general, these longer periods contained significantly more whips although whip rate was lower in triads for three of the five retreat display periods. (Table 2.7).

As Table 2.8 indicates, at least some of this increase in duration of triadic retreat display periods was brought about by an increase in the number of vacillations performed by the courter. This latter response is apparent for all triadic retreat display periods, but attained statistical significance in only two.

3. Spermatophore Transfer Behaviour. The relevant data are presented in Table 2.9. The timing of events immediately before and after spermatophore deposition was not affected by the presence of another male.

4. Encounter Duration. Out of 28 dyads observed, 16 were of two sequences and 12 of three sequences duration. For the 46 triads, the respective figures were 28 and 18.

There was no difference in the relative proportion of each encounter duration for dyadic and triadic tests ($\chi^2 = 0.1$, $P > 0.05$).

| Scores | 2 sequence encounters: | | 3 sequence encounters: | |
|------------------------|------------------------|---------------------|------------------------|---------------------|
| | dyadic (N = 16) | triadic (N = 28) | dyadic (N = 12) | triadic (N = 18) |
| number of fan bouts | 1.68 ± 3.16 | 2.03 ± 4.18 | 1.83 ± 2.45 | 1.90 ± 3.80 |
| | NS | | NS | |
| total fan duration (s) | 11.80 ± 2.40 | 19.80 ± 2.93 | 14.20 ± 1.51 | 22.50 ± 3.20 |
| | P < 0.05 | | P < 0.05 | |
| number of waves | 13.91 ± 1.90 | 12.00 ± 1.10 | 13.80 ± 1.10 | 14.00 ± 0.83 |
| | NS | | NS | |
| number of whips | 5.03 ± 0.51 | 3.20 ± 0.50 | 5.00 ± 0.72 | 3.03 ± 0.53 |
| | NS | | P < 0.05 | |

Table 2.5 Four scores of male display during the 60 second static display period (mean ± SEM) for dyadic and triadic encounters. Scores compared using the t-test.

| retreat display duration (s) | 2 sequence encounters: | | 3 sequence encounters: | |
|------------------------------|------------------------|---------------------|------------------------|---------------------|
| | dyadic (N = 16) | triadic (N = 28) | dyadic (N = 12) | triadic (N = 18) |
| 1st sequence | 9.60 ± 1.20 | 27.00 ± 3.40 | 13.40 ± 2.20 | 30.40 ± 2.90 |
| | P < 0.001 | | P < 0.001 | |
| 2nd sequence | 16.20 ± 2.40 | 39.01 ± 3.90 | 12.30 ± 1.91 | 30.40 ± 4.90 |
| | P < 0.001 | | P < 0.001 | |
| 3rd sequence | - | - | 27.30 ± 2.90 | 50.00 ± 6.02 |
| | | | P < 0.001 | |

Table 2.6 The duration of retreat display periods (mean ± SEM) for dyadic and triadic encounters. Scores compared using the t-test.

| Scores | 2 sequence encounters: | | 3 sequence encounters: | |
|---------------------------|--------------------------|---------------------|---------------------------|---------------------|
| | dyadic (N = 16) | triadic (N = 28) | dyadic (N = 12) | triadic (N = 13) |
| number of whips: | | | | |
| 1st sequence | 2.80 ± 0.40 P < 0.001 | 5.20 ± 0.50 | 3.00 ± 0.43 P < 0.001 | 6.70 ± 0.93 |
| 2nd sequence | 4.31 ± 1.20 P < 0.005 | 8.51 ± 1.04 | 3.05 ± 1.20 NS | 5.30 ± 0.92 |
| 3rd sequence | - | - | 7.33 ± 1.50 P < 0.05 | 10.80 ± 1.40 |
| whip rate (no./100 s): | | | | |
| 1st sequence | 33.40 ± 3.25 P < 0.05 | 23.16 ± 1.90 | 25.15 ± 1.71 NS | 20.60 ± 1.83 |
| 2nd sequence | 29.80 ± 2.64 NS | 23.66 ± 2.17 | 27.80 ± 2.29 NS | 23.11 ± 2.16 |
| 3rd sequence | - | - | 26.04 ± 1.47 P < 0.005 | 21.43 ± 1.28 |

Table 2.7 Two scores of male display during retreat display periods (mean ± SEM) for dyadic and triadic encounters. Scores compared using the t-test.

| sequence in encounter | 2 sequence encounters: | | 3 sequence encounters: | |
|-----------------------|------------------------|---------------------|------------------------|---------------------|
| | dyadic (N = 16) | triadic (N = 28) | dyadic (N = 12) | triadic (N = 18) |
| 1st | 0.25 ± 0.45 | 0.89 ± 1.14 | 0.38 ± 0.65 | 0.63 ± 1.12 |
| | P < 0.05 | | NS | |
| 2nd | 0.73 ± 1.50 | 1.32 ± 1.40 | 0.61 ± 0.65 | 0.95 ± 1.12 |
| | NS | | NS | |
| 3rd | - | - | 0.84 ± 0.80 | 1.85 ± 1.04 |
| | | | P < 0.01 | |

Table 2.8 The number of vacillations during retreat display periods (mean ± SEM) for dyadic and triadic encounters. Scores compared using the t-test.

| sequence in encounter | 2 sequence encounters: | | 3 sequence encounters: | |
|-------------------------|------------------------|--------------------------|------------------------|---------------------|
| | dyadic (N = 16) | triadic (N = 28) | dyadic (N = 12) | triadic (N = 18) |
| <u>1st</u> | | | | |
| creep → depo- sition | 6.00 ± 0.40 | 6.02 ± 0.26 NS | 7.00 ± 0.41 | 6.00 ± 0.43 NS |
| deposition → retreat | 15.01 ± 1.40 | 19.00 ± 1.73 NS | 18.04 ± 1.30 | 15.00 ± 1.61 NS |
| <u>2nd</u> | | | | |
| creep → depo- sition | 5.01 ± 0.30 | 6.00 ± 0.33 P < 0.05 | 7.00 ± 0.55 | 7.11 ± 0.60 NS |
| deposition → retreat | 28.10 ± 1.61 | 24.11 ± 1.06 P < 0.05 | 24.00 ± 1.16 | 21.04 ± 1.46 NS |
| <u>3rd</u> | | | | |
| creep → depo- sition | - | - | 7.10 ± 0.60 | 7.01 ± 0.40 NS |
| deposition → retreat | - | - | 32.03 ± 2.50 | 34.03 ± 2.60 NS |

Table 2.9 The timing(s) of spermatophore transfer behaviour (mean ± SEM) for dyadic and triadic encounters. Scores compared using the t-test.

Discussion

Data on the temporal patterning of male sexual behaviour in dyads and triads are schematically summarized in Figure 2.7. In the presence of a potential rival, a courting male alters certain aspects of both the content and timing of his behaviour. During static display, he increases the duration of fan display which he performs to the female. Retreat displays are longer in the presence of a rival, and contain more whip display. Part of this increase in duration is brought about by an increase in the number of times the male vacillates between retreat display and the initial stages of spermatophore transfer behaviour. However, the timing of the male's behaviour during the spermatophore transfer phase of a sequence is not affected by an extra male. Neither is the number of sequences completed by the courter.

I suggest that these changes in the courting male's behaviour in the presence of another male are best interpreted as defenses against the threat of sexual interference (the behaviour of the potential rival in triad tests varied from apparent indifference to sexual interference). Considering first static display, Halliday and Houston (1978) found that the total amount of fanning performed by a male in a dyad is correlated with the number of spermatophores he is able to deposit. By fanning for longer in the presence of a rival, the courter may be attempting to stimulate the female to such an extent that she ignores other males; indeed, fanning is believed to stimulate the female olfactorily and 'persuade' her to mate (Halliday 1975a; Arnold and Houck 1982). In the guppy *Poecilia reticulata*, males display at a higher rate when courting females in the presence of rivals (Farr 1976), a situation which seems analogous to the case of the newt.

Secondly, by increasing the duration of retreat display periods in triads, the courter is able to stimulate the female with more whip display,

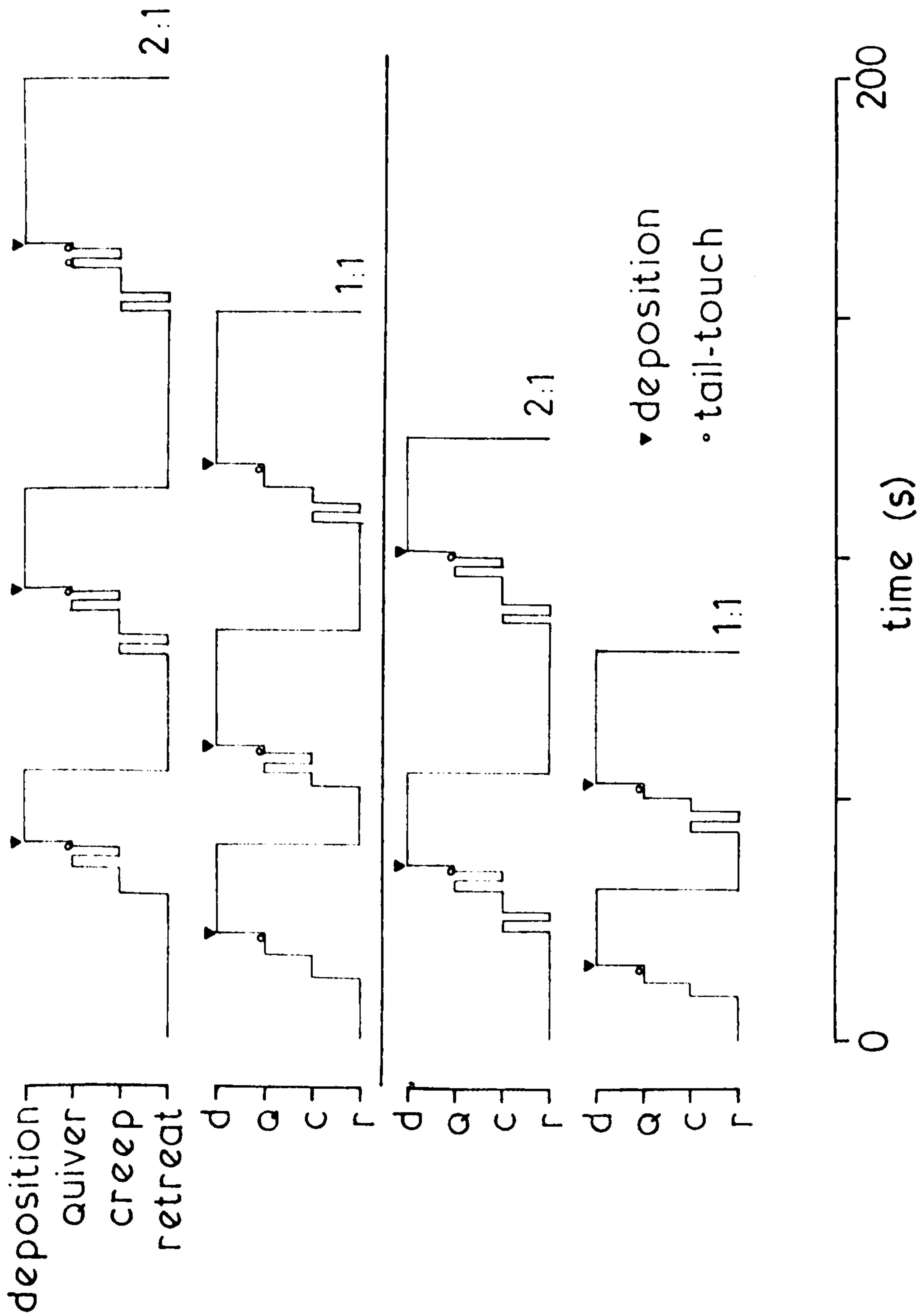


Figure 2.7 Highly schematic representation of the temporal patterning of sexual behaviour in dyadic and triadic encounters of two (bottom) and three (top) sequences in duration. The sequences are based on mean data and all scores have been rounded to the nearest whole number.

and may also be attempting to draw her away from the proximity of the other male. In all salamandrid urodeles, except those in the genera *Triturus* and *Cynops*, courtship includes a period of amplexus, in which the male physically monopolizes his mate (Arnold 1977; Halliday 1977a). Because such monopolization is not possible in the smooth newt, it is difficult for the courter to defend the female against sexually interfering males. Drawing her away from a rival (with her cooperation, of course) may be the best that he can do. In the salamander *Ambystoma tigrinum*, males appear to show a behaviour functionally analogous to retreat display as a form of sexual defense; the courting male will push the female away from a rival with his snout (Arnold 1976). As with retreat display, this pushing action is also seen in dyadic encounters.

Thirdly, as the courter leads the female during retreat display, he can easily see the whereabouts of other males in the vicinity. When he turns away from the female in order to initiate spermatophore transfer behaviour, he cannot be sure that it is the female, and not a rival male, who is about to nudge his tail and thus elicit the deposition of a spermatophore. I suggest that by vacillating more often in a potentially competitive situation, the courter is 'checking' that it really is the female behind him. Such an action would seem to have obvious adaptive significance in view of the fact that sexually interfering males mimic female behaviour (as described in Chapter 2.4.1).

Thus, I suggest that male smooth newts have evolved a number of actions which are used in defense against sexual interference. These actions include an increased intensity of courtship display, a drawing of the female away from a rival and a 'checking' action during the transition from retreat display to spermatophore transfer behaviour.

In causal terms, the results of this experiment raise some interesting points. Using the multivariate technique of principal components analysis, Halliday (1976) characterized courtship sequences as either of high or low 'libido', depending on the nature of the male's behaviour. In high libido sequences, fanning occurs at a high rate during static display, retreat display periods are brief and vacillation is infrequent. During low libido sequences, fan rates are low, retreat display periods are longer and vacillations are more frequent. The triadic courtships described above seem to be 'mosaics' of high and low libido characteristics. The male's behaviour during static display is characteristic of high libido, whereas the longer retreat display periods and greater number of vacillations are typical of low libido. On the face of it, this finding raises doubts as to the validity of considering libido as an unitary phenomenon. As discussed in Chapter 2.2, various factors influence the sexual behaviour of the male smooth newt, such as his sperm and oxygen supplies and the responsiveness of his partner. To this list can now be added an influence of the immediate social environment, namely the presence of a potential rival.

The description of sexual defense given above is really an 'average' response to the presence of a rival male; in some tests, the rival sexually interfered, in others he did not. It would be instructive to separate the data presented here in order to determine how sexual defense varies with the behaviour of the rival. This has not been done because it would involve a reduction in the sample sizes of the triad tests observed.

In summary, the results presented in Chapters 2.4 and 2.5 of this thesis provide evidence for the coevolution of sexual interference and sexual defense in male smooth newts. However, as Darwin (1871) clearly recognized and as Halliday (1983) has recently stressed, mating competition and mate choice often occur together and interact within a single mating

system. Mate choice in the smooth newt is considered in Chapter 2.7.

In the next experiment, I shift my attention to female smooth newts, and investigate the extent to which females engage in multiple mating and the possible consequences of such activity.

2.6 Multiple Mating by Female Smooth Newts

In Chapter 2.4.1, evidence was presented which demonstrated that sexual interference may sometimes lead to a female becoming inseminated by two males (first the courter, then the rival) in rapid succession. As discussed more fully by Halliday and Verrell (1983) and in Chapter 5.2.2 of this thesis, multiple insemination may result in sperm competition. The latter is said to occur when sperm from two or more males compete for the opportunity to fertilize a female's ova (Parker 1970). In this section, I describe an experiment designed to test the hypothesis that female smooth newts mate with more than one male between the beginning of the breeding season and the onset of oviposition.

Method

This experiment was conducted in the spring breeding season of 1981, and used females captured in pit-fall traps as they migrated to their breeding pond. It was assumed that these females had not yet been inseminated.

Twenty five females were each paired with a male and were permitted to pick up a single spermatophore (the initial insemination). Each was then placed with a male known to be sexually responsive (as determined by his response to a female held in a strait jacket; see Chapter 2.5) for 30 minutes at fixed intervals after the initial insemination. These

intervals were of one hour, 12 hours and two, four, eight, 16 and 20 days. Not all females were tested at every interval.

The response of each female during the 30 minute trials was classified according to the following qualitative scale:

1. no positive response.
2. weak positive response.
3. at least one spermatophore deposition elicited, but no pick up.
4. at least one spermatophore picked up.

Results

The results of this experiment are presented in Table 2.10. Some females remained sexually responsive for at least 20 days after their initial insemination. Forty four per cent were responsive enough to elicit spermatophore deposition, although only 8 per cent were multiply inseminated.

Discussion

These data suggest the possibility that female smooth newts can build up a stock of sperm to which several males make a contribution. It is thus also possible that sperm competition occurs in the female genital tract and that the paternity of a clutch of ova may be shared. Although none of the females used in this study actually laid any eggs, J.M. Roberts (unpublished data) has found that females will remate between periods of oviposition.

In many animal species, females become unresponsive to further male courtship after insemination. The female may literally "switch herself

| Time since last sperm- atophore picked up | Number of females that: | | | |
|--|-------------------------|----------------------------|---|-----------------------------------|
| | showed no response | showed weak response | elicited spermatophore deposition | picked up a sperm- atophore |
| 1 hour | 17 | 4 | 1 | 0 |
| 12 hours | 17 | 2 | 2 | 1 |
| 2 days | 22 | 1 | 0 | 1 |
| 4 days | 21 | 0 | 1 | 0 |
| 8 days | 24 | 0 | 1 | 0 |
| 16 days | 21 | 1 | 2 | 0 |
| 20 days | 22 | 1 | 2 | 0 |

NOTE Not all of the 25 females were tested at all time intervals.

Table 2.10 The responses of a group of 25 inseminated females to further male courtship.

off", as in some butterflies (Wiklund 1982) or may be rendered unresponsive by some action of the male, e.g. the garter snake, in which the male applies an 'antiaphrodisiac' to the female (Ross and Crews 1978). Female smooth newts are apparently not rendered totally unresponsive after insemination, but whether they gain any advantage from multiple insemination is not clear. Walker (1980) suggests that it may permit females to increase between-sibling genetic heterogeneity in their progeny and/or might act as an "insurance policy" against matings with subfertile males (see also Knowlton 1983). Remating after a period of oviposition may be of use if the female has more eggs to fertilize but not enough sperm to do so. In those insects in which males transfer nutrients as well as sperm in their ejaculates, remating by females may be a nutritional rather than sexual strategy (Wiklund 1982). Male newts are thought to provide only sperm at mating, but this has yet to be empirically verified.

The gain for a male who mates with an inseminated female depends on the fate of the sperm that he transfers. If the sperm from successive males mix in the female or the last male to mate displaces the sperm from previous males, he may gain at least some fertilizations (see Chapter 5.2.2). Data on the fate of sperm in the genital tract of the female smooth newt are not available.

2.7 Mate Choice in the Smooth Newt

As discussed in Chapter 2.2, Halliday (1977a) has suggested that both male and female newts may be choosy concerning who they accept as mates, and has envisioned one of the functions of courtship as facilitating the assessment of each individual by the other. Specifically, Halliday suggests that partners may select one another on the basis of body size, which is correlated with age (Bell 1977, but see Hagstrom 1980b).

Females might choose larger, older males if such males are particularly fecund or if an ability to survive reflects general fitness. Males might prefer larger, older females for similar reasons, although the fact that female fecundity is related to body size (Bell 1977) is probably of greater importance.

The experiments described here were designed to investigate Halliday's hypothesis concerning size-based mate choice in the smooth newt.

2.7.1 Female Mate Choice

The hypothesis tested was that females prefer larger males as mates.

Method

This experiment followed the same design and procedure as that described in Chapter 2.4.2 for female responses to male density, where proximity was used as an index of choice.

Females were given a choice between two males differing by at least 5 mm in length and 0.5 g in weight. Twenty four different females were tested.

Results

The histograms in Figure 2.8 summarize the relevant data. It is quite apparent that females show no general preference for larger males over smaller ones.

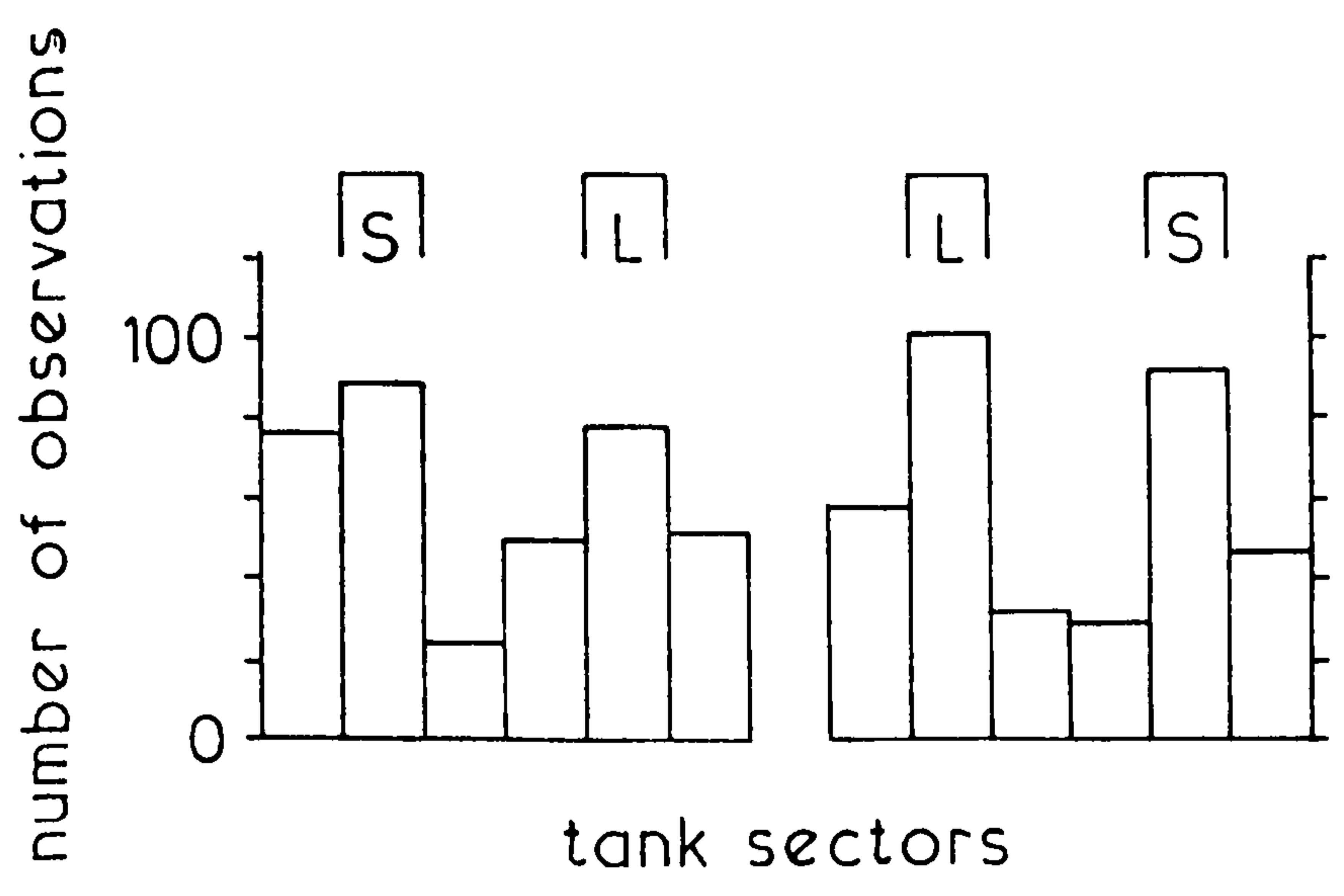


Figure 2.8 Histograms showing the responses of females to small (S) and large (L) males.

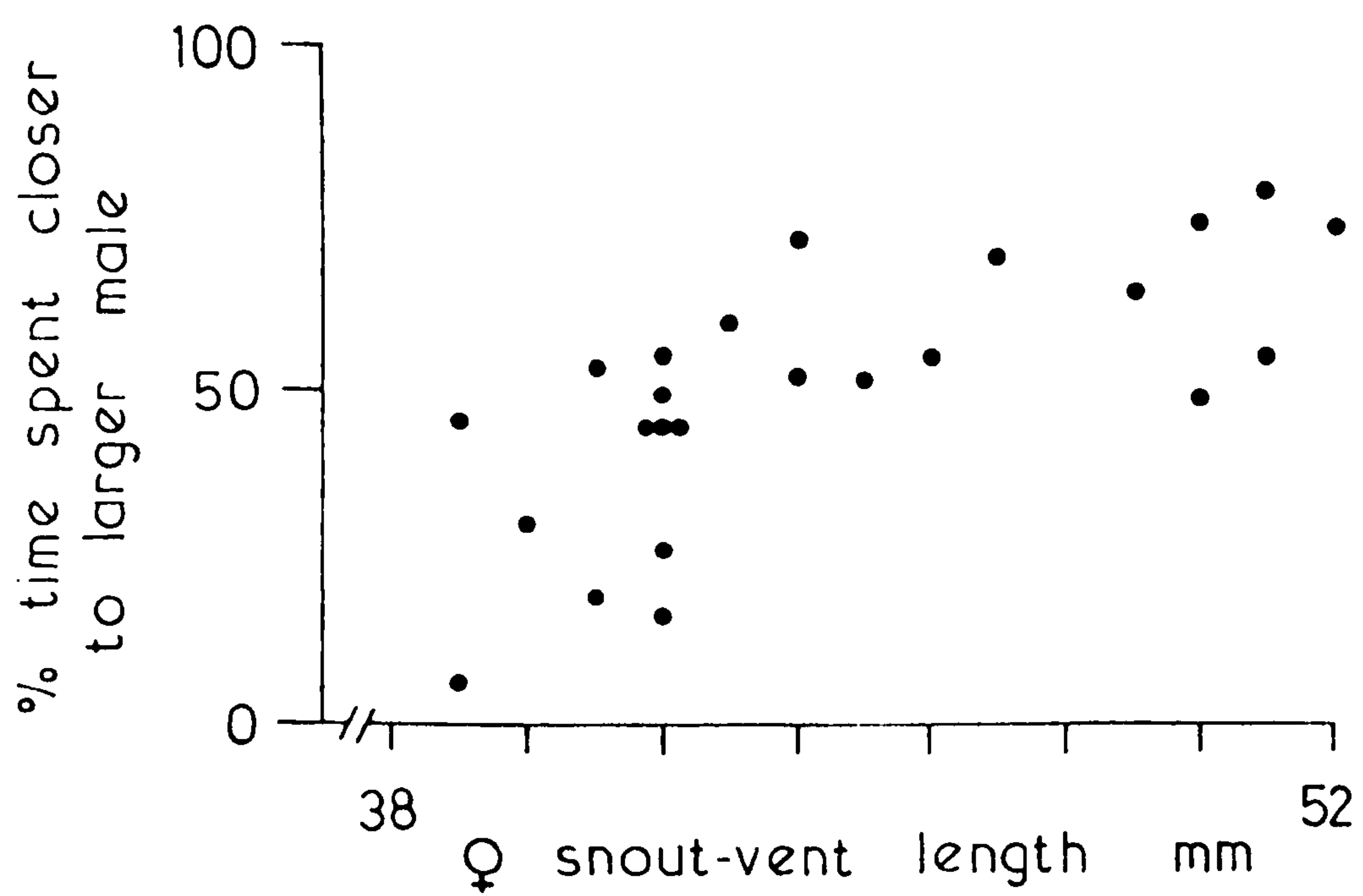


Figure 2.9 The relationship between female length and the proportion of time spent closer to the large of two males. Taken from the data presented in Figure 2.8.

However, these data were then further analyzed and, as shown in Figure 2.9, the amount of time that a female spent closer to the larger of the two males was positively correlated with her length ($r_s = 0.72$, $P < 0.001$). There was a tendency for females to remain in the proximity of males reasonably matched to themselves in body length, i.e. for their preference to be assortative with respect to body length.

2.7.2 Male Mate Choice

The hypothesis tested was that male newts select larger, more fecund females as mates.

Method

This experiment employed the same design and procedure as that described in Chapters 2.4.2 and 2.7.1. Males were given a choice between two females differing by at least 5 mm in length and 0.5 g in weight. A total of 22 different males were tested.

In order to verify that female fecundity is correlated with body size, 30 females of known size were sacrificed and the number of yolked oocytes in the ovaries counted. Bell (1977) suggests that yolked oocytes are the only developmental stage of ovum available for fertilization in any one breeding season. As these females were captured in pit-fall traps before they reached their pond, it was assumed that they contained their full yolked oocyte complement for the breeding season.

Results

The proximity preferences of male newts are shown as pooled data in the histograms in Figure 2.10. The non-parametric sign-test was used to

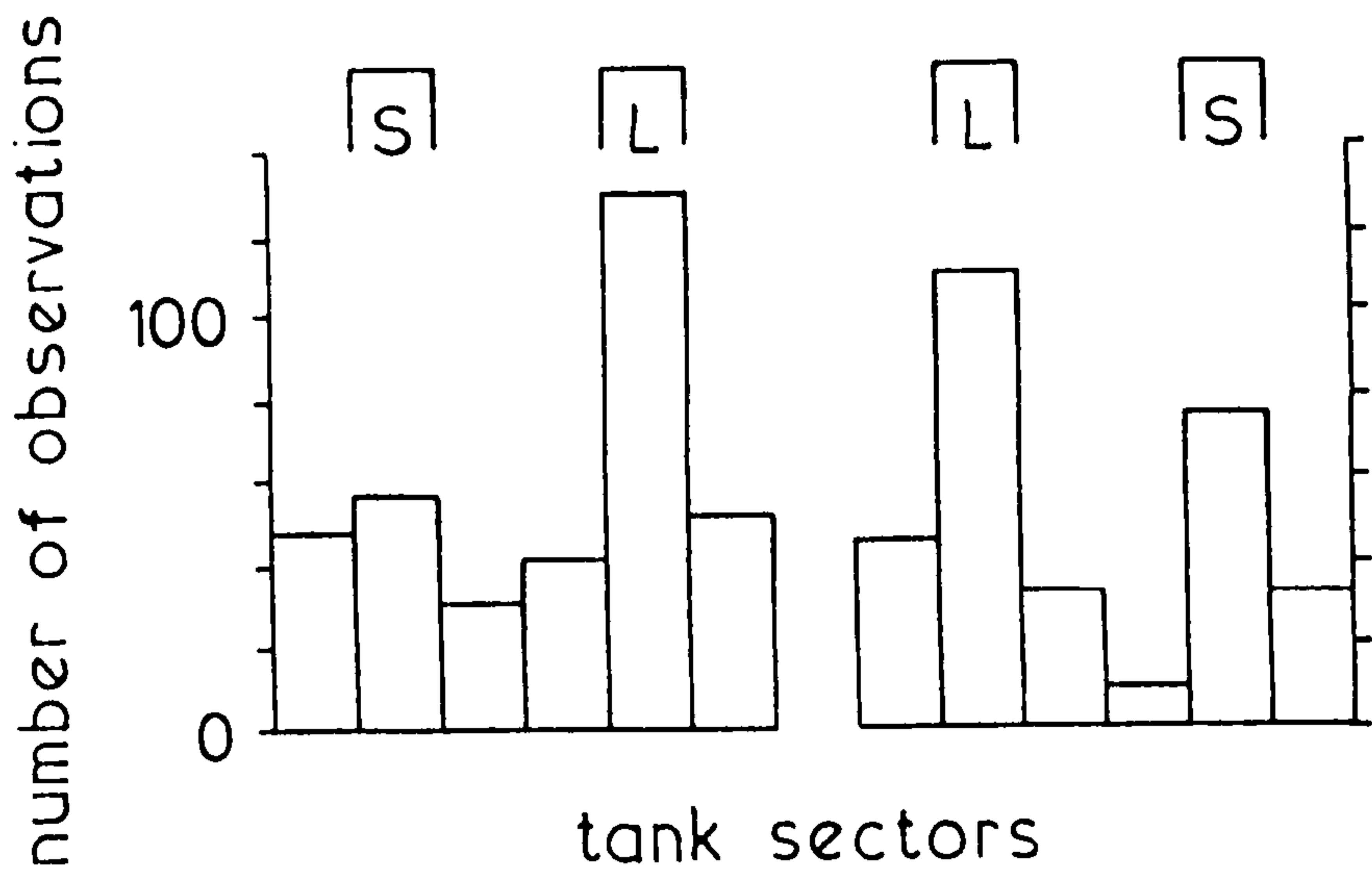


Figure 2.10 Histograms showing the responses of males to small (S) and large (L) females. Statistical analysis of these data is presented in Table 2.12.

| | |
|----------------------------|----------------------------|
| Small female, large female | Large female, small female |
| P < 0.019 | P < 0.019 |

Table 2.11 Results of sign-tests conducted on the raw data for individual males which are summarized as histograms in Figure 2.6.

examine the data for individual males. As is shown in Table 2.11, males spent significantly more time in the vicinity of the larger of the two test females available.

A significant positive correlation was found between both female length and egg number ($r = 0.68$, $P < 0.001$; see Figure 2.11) and female weight and egg number ($r = 0.78$, $P < 0.001$). Thus female fecundity was size-related in these newts.

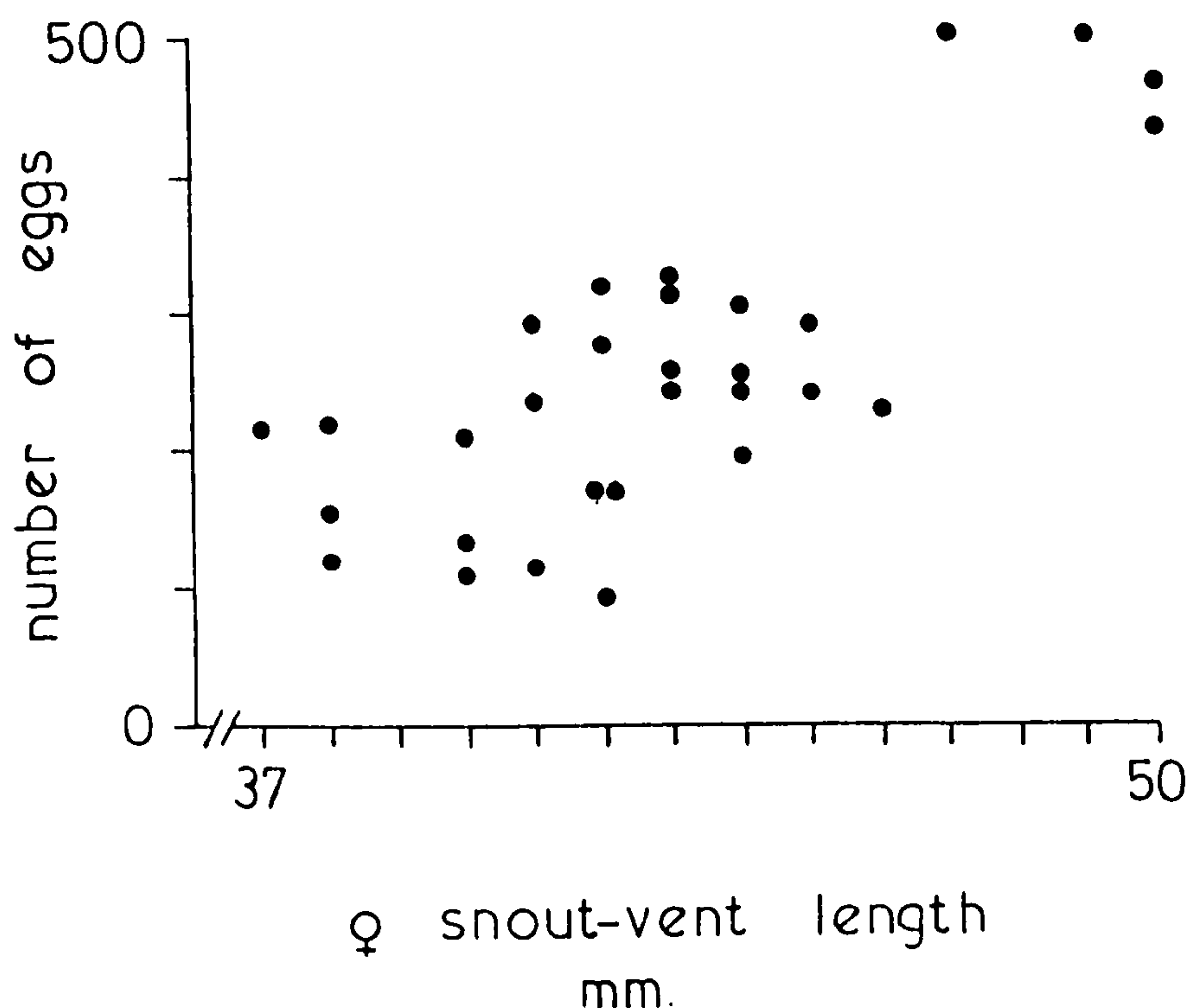


Figure 2.11 The relationship between female length and the number of yolked oocytes in the ovaries.

2.7.3 Discussion

That males prefer larger, more fecund females as mates is in accord with the original hypothesis of Halliday (1977a). He believed that the male assesses female fecundity during the initial orientation phase of a sexual encounter, using both olfactory cues (for female "ripeness") and tactile feedback from her swollen belly. The experimental design used

here permitted males visual cues only, and yet they could still discriminate between females of different sizes (see Chapter 4.4).

The hypothesis that females prefer larger males is not supported by the data obtained here. Unlike males, females seem to prefer males reasonably matched to their own body size, resulting in a tendency towards size-assortative preference.

Despite the rather artificial nature of these experiments and some uncertainty about whether proximity preference really reflects mate choice, some 'guarded speculation' as to the significance of these results seems justified. By choosing more fecund mates, males may enjoy a high rate of fertilization, and this has obvious adaptive value. But why are female preferences size-assortative? The answer to this may be in the spatial dynamics of courtship behaviour. During the spermatophore transfer stage of a sequence, the male moves away from his spermatophore for a distance of one snout-vent body length (Halliday 1974). If the female follows him closely, her cloaca comes to be in the close vicinity of the spermatophore. Although my data are insufficient to test this hypothesis, I suggest that the probability of spermatophore pick up may be greater if males and females are matched for length. If this assertion is correct, then females choose their males on the basis of ease of insemination, and arguments for choice of 'good genes' and the heritability of fitness are not required (Halliday 1983).

To take this argument further, let us assume that these preferences are expressed in nature. If a small but sexually active male encounters a large female, he should be stimulated to court her (because of her large size) whereas she should be selected to resist him (because of the disparity in their sizes). The result is thus a conflict over mating decisions, as theoretically modelled by Parker (1979, 1983). Such a

conflict occurs in the toad *Bufo bufo*, where optimum mate size is different for the two sexes. In this species, observed pairings fall in between the male and female optima (Davies and Halliday 1977), although it is not clear whether mate choice is responsible for the pattern observed.

Evidence for such a conflict in smooth newts was not obtained in the experiments reported in this thesis. The hypothesis is, however, empirically testable; for instance, encounters between large males and large females (satisfying the requirements of both partners) should occur with less conflict than any other pattern of pairing. The exact nature of this conflict cannot be predicted at present, but may be reflected in scores such as latency to initiate courtship, number of sequences completed or pick up success. Sexual conflict in the smooth newt will be investigated further in future breeding seasons.

2.8 An Overview of Sexual Selection in the Smooth Newt

The evidence presented in this Chapter is in agreement with the hypothesis that sexual selection has influenced the evolution of the sexual behaviour of the smooth newt. Both intermale competition and male and female mate choice are operative in the mating system of this species. Much of the evidence has been evaluated at the end of each section in this Chapter, and some points are discussed further in Chapter 5. In this section, sexual selection in the smooth newt is discussed in the broader context of contemporary thought concerning sexual selection.

Halliday (1983) has recently reviewed a number of conceptual problems that arise from studies of sexual selection. For several of these problems, I shall demonstrate how our knowledge of the smooth newt contributes to their clarification.

2.8.1 The Benefits and Criteria of Mate Choice

Animals may choose their mates on the basis of a number of criteria. Similarly, they may benefit from mate choice in several ways. Many animals, including the male newt, choose larger, more fecund individuals as mates, thus ensuring the fertilization of as many ova as possible. Choice in the female newt is more complex: she will mate selectively with males able to produce large numbers of spermatophores (Halliday 1974) and prefers males which may be more efficient at sperm transfer due to their size.

These different criteria for males and females may sometimes lead to a conflict over mating decisions, for the optimum partner size for each individual in a pair may not coincide.

2.8.2 The Functions of Epigamic Characters

Darwin (1871) described the greater adornment of the breeding male newt and attributed the evolution of its epigamic characters to sexual selection. Halliday (1983) has stressed that, contrary to popular belief, the epigamic characters of the males of many species are used more in intermale competition than as a basis for mate choice. In the newt, no evidence has been obtained to implicate the male's epigamic characters in either capacity. It is possible that they function more in terms of sexual isolation (e.g. species recognition) than sexual selection but this has yet to be empirically investigated. Some evidence for this interpretation comes from the fact that the male's secondary sexual characteristics are most developed in areas where the smooth newt is sympatric with other *Triturus* species (Arnold and Burton 1978).

2.8.3 Mate Choice and Male Competition

Although Darwin (1871) differentiated between the two components of differential mating success, Halliday (1983) has stressed that they are not distinct, mutually exclusive processes. Both sexual interference and male and female mate choice operate in the smooth newt, and it seems probable that the former may thwart the effective expression of the latter. However, the exact nature of the interactions between competition and choice awaits further study.

2.8.4 Females may Mate with Several Partners

Female smooth newts may engage in multiple mating, both because they remate before they initiate egg laying and due to sexual interference. If sperm competition results, this can affect the ability of one or more of the males with whom the female mates to fertilize her ova. Sperm competition may also affect female reproductive success if it leads to fertilization by 'high quality' males.

CHAPTER 3

THE SEXUAL BEHAVIOUR OF THE RED-SPOTTED NEWT,
NOTOPHTHALMUS VIRIDESCENS

CHAPTER 3

THE SEXUAL BEHAVIOUR OF THE RED-SPOTTED NEWT, *NOTOPHTHALMUS VIRIDESCENS*

In this Chapter, I review existing literature on the natural history (Chapter 3.1) and sexual behaviour (3.2) of the red-spotted newt. I then present an analysis of the courtship behaviour of this species during encounters between one male and one female, a dyad (3.4). This is followed by a consideration of the interactions between locomotor and sexual activity and breathing in male newts (3.5). The Chapter finishes with a discussion of the behaviour of the red-spotted newt in the context of other urodele amphibians, and other animals with similarly complex courtship behaviour (3.6).

3.1 The Natural History of the Red-Spotted Newt

The red-spotted newt, *Notophthalmus viridescens viridescens* (Rafinesque), is a common salamandrid urodele of the eastern states of North America, where it occurs in sympatry with three other subspecies (Conant 1975). In most parts of its range, the adult newt spends much of the year living a terrestrial existence, when it can be found under logs and rocks in woodland areas. The major breeding season begins in the spring as the weather becomes milder (Healy 1975, Hurlbert 1969). The adult is philopatric and tends to return to the same breeding pond season after season. Both visual and olfactory cues are used in 'pond imprinting' and homing (Hershey and Forester 1980). Ponds preferred as breeding sites tend to be higher in elevation, farther from woodland and deeper than unutilized ponds. Muddy bottoms and turbid water are also apparently favoured (Gates and Thompson 1982).

Outside of the breeding season, the newt is adapted for life on land. At the onset of the season, a number of changes occur which equip the newt for its life in water. These very much resemble the opposite of those changes shown by the juvenile newt when it leaves the water for the first time, and are known collectively as 'second metamorphosis'. The hormones prolactin and thyroxine are responsible for this suite of changes, together with a contribution from the sex steroids (for a review, see Ensor 1978).

One obvious change is in the shape of the tail, which becomes dorso-ventrally deeper and laterally compressed. Shaped like this, it is better able to produce the propulsive force necessary for swimming. This change is most marked in the male.

The skin changes from a rough, dry surface to a smooth, slippery one. In the water, the skin is used as an accessory respiratory surface, supplementing aerial gas exchange. It probably also plays a role in

ionic and osmotic regulation. The skin is periodically shed in the water, the exuvia being eaten.

On land, the epithelium lining the buccal cavity is ciliated, but the cilia are lost when the newt is in its aquatic phase. In its deciliated state, the epithelium acts as another respiratory surface.

The pigment of the retina also changes, from one typical of land vertebrates to one typical of aquatic forms (Crim 1975).

Halliday (1972) has reviewed a number of other changes which occur in the European smooth newt (*Triturus vulgaris*) as it prepares to breed, including changes in the morphology of the nares and mouth, and the recrudescence of the neuromast lateral-line system. Similar changes have not been reported in the red-spotted newt, but seem likely to occur.

The secondary sexual characteristics also develop at the beginning of the breeding season. The body of both sexes is olive green in colour, paling to a straw colour on the belly. The female often appears a little darker than the male, although the body of both is flecked with dark speckles. A variable number and pattern of dorsolateral red spots, ringed in black, is found in both sexes. Newts which are about to shed their skins are duller in colour.

The male has a dorsal crest which begins about half way down the midline of his dorsum and extends backwards as a vertical extension of his tail. The free edge of this crest varies from being smooth to gently undulated. The male's hindlimbs are much broader and thicker than those of the female, and black pads of cone-shaped, cornified cells develop on the toes, plantar region and inner thigh in the male (Singhas and Dent 1975). These limbs are used to grasp the female during courtship and the pads

undoubtedly serve to give the male a better grip on the female. Pads similar in function occur in several other urodele species as well as some anurans (Arnold 1977).

As in all amphibians, the skin of the red-spotted newt is richly endowed with glands (see Madison 1977, Elkan and Cooper 1980). The male has an odoriferous gland in his cloaca and a number of specialized glands on his cheeks, visible as three pits behind each eye. These glands produce a number of glycoproteinaceous secretions (Benson 1964). The female also has similar cheek glands, but in her they are less well developed.

Finally, the male's cloaca is larger and more rounded than that of the female. That of the male contains a dorsal gland, which produces odours, and pelvic and ventral glands, which produce the spermatophore (Sever 1981). It also bears a fringe of pale pink papillae. The female's cloaca is more cylindrical in shape and bears an outer rim of cornified cells similar to those on the male's hindlimbs; this rim of cells probably facilitates the attachment of the spermatophore to the cloacal region (Zimmer and Dent 1981).

With all of these changes complete, the newt is ready to breed. Males arrive at the breeding site before females (Humbert 1969) and the adult sex ratio tends to be skewed towards an excess of males (up to 2:1). This was thought to be a consequence of greater female mortality (Gill 1979), but is now believed to be a combined result of sampling error and the fact that females do not breed every year. They may do this because of the debilitating effects of infection with pathogenic trypanosomes (Gill and Berven, in press). Both males and females have a median life expectancy of three breeding seasons, and the annual survival of adults has been estimated as about 0.83.

During the breeding season, the newts vacillate between water and land, due to thermal stress and/or the presence of blood-sucking leeches which transmit trypanosomes (Gill 1978a). When in the water, the newts tend to remain in the vicinity of rooted water plants (Burton 1977, Premo 1982). Healy (1974) suggested that there may be some degree of spatial segregation of the sexes, but Harris (1981) has experimentally demonstrated that males 'cruise' the entire pond, actively searching for mates rather than showing any sort of site tenacity.

The red-spotted newt is an opportunistic feeder, with a catholic range of acceptable foods. Prey are selected by both sight and smell (Wood and Goodwin 1954) and are seized in the jaws. In the laboratory, feeding efficiency is reduced if the water is turbid (Attar and Maly 1980) and if dead prey are given, stressing the importance of vision.

Egg laying begins between 14 and 21 days after insemination (Pope 1924). D.E. Gill (personal communication) suggests that females produce a steady stream of ova throughout the breeding season, with up to 250-300 eggs per female. Larger and older females produce larger clutches (Pike 1886). Each egg is wrapped individually in the curled leaf of a water plant, in bouts of 6-10 eggs at a time. Each deposition takes from 5-10 minutes to complete, and is restricted to the light phase of the light-dark cycle (Pope 1924).

Once an egg is laid, the female takes no further interest in it. Hatching occurs after about 21 days and the resulting tadpole larvae remain aquatic for several months. They are solely carnivorous and become more active as they get older. The larval population in a pond is very sensitive to abiotic fluctuations in the local environment, especially drought, and may be heavily predated by leeches (Gill and Berven, in press).

The timing of larval metamorphosis is variable and appears to be dependent on climate, as harsh weather results in its delay. Not all larvae transform in their first summer; some overwinter in the water and transform in the following year. After metamorphosis, the newt leaves the water, its migration to and on land being very sensitive to humidity. The transformed newt is now a juvenile known as an eft. Healy (1975) recognizes three stages of juvenile life:

1. migration to land
2. residence on land
3. second metamorphosis and the first breeding migration to water.

When residing on land, the eft tends to move about very little, although mass movements may sometimes follow heavy rainfall (Petranka and Phillippi 1979). Both activity and habitat selection are greatly influenced by the availability of food which includes small invertebrates such as annelids, arachnids and insects (Macnamara 1977). Efts are commonly found under rocks and logs in woodland. In some areas, efts may acquire aposematic red colouration, which advertises their toxicity to potential predators (Brandon, Labanick and Huheey 1979).

In the harsh coastal regions of Massachusetts, the eft stage may be omitted from the life cycle. Instead, the larva remains in the water, growing rapidly and reaching sexual maturity before its terrestrial eft counterpart elsewhere. Some degree of neoteny may also occur in these populations (Healy 1973).

Most adults leave the water at the end of the breeding season, in the late summer, although some overwinter in the pond (Pitkin and Tilley 1982). There is, however, a great deal of variation between populations

in the annual cycle of behaviour, and in some areas, adult newts never leave the water after their initial second metamorphosis (D.E. Gill, personal communication). One interesting variation on the general cycle described above is the existence in some areas of a breeding migration in the autumn. Although adults captured in the water at this time will court vigorously, inseminated females do not lay eggs; they may store sperm from these matings in their spermathecae over the winter, in order to fertilize their eggs early in the next spring (D.M. Sever, personal communication). Hurlbert (1969) has found that the autumn migrants consist primarily of efts about to make their first breeding effort, and Bell (1977) has described a similar migration of juveniles in the smooth newt in England.

The annual cycle of adult behaviour is closely correlated with concurrent changes in the gonads of both sexes. Considering only adults that she captured in water, Adams (1940) found that by the end of the spring breeding season, the gonads are very much depleted of mature gametes. By the autumn, the male gonads are replete with mature sperm, suggesting that a period of intense gametogenesis follows the end of the spring season (see Lofts 1974). The testes remain in this mature state over the winter and the newts are thus ready to breed as soon as environmental conditions allow in the following spring (see Figure 3.1).

Sensory Capacities

In any study of animal communication, it is necessary to have some understanding of the sensory capacities of the animals under investigation. In the red-spotted newt, these are complex.

Vision is important in the feeding behaviour of the newt (Wood and Goodwin 1954, Attar and Maly 1980). Adults are positively phototactic

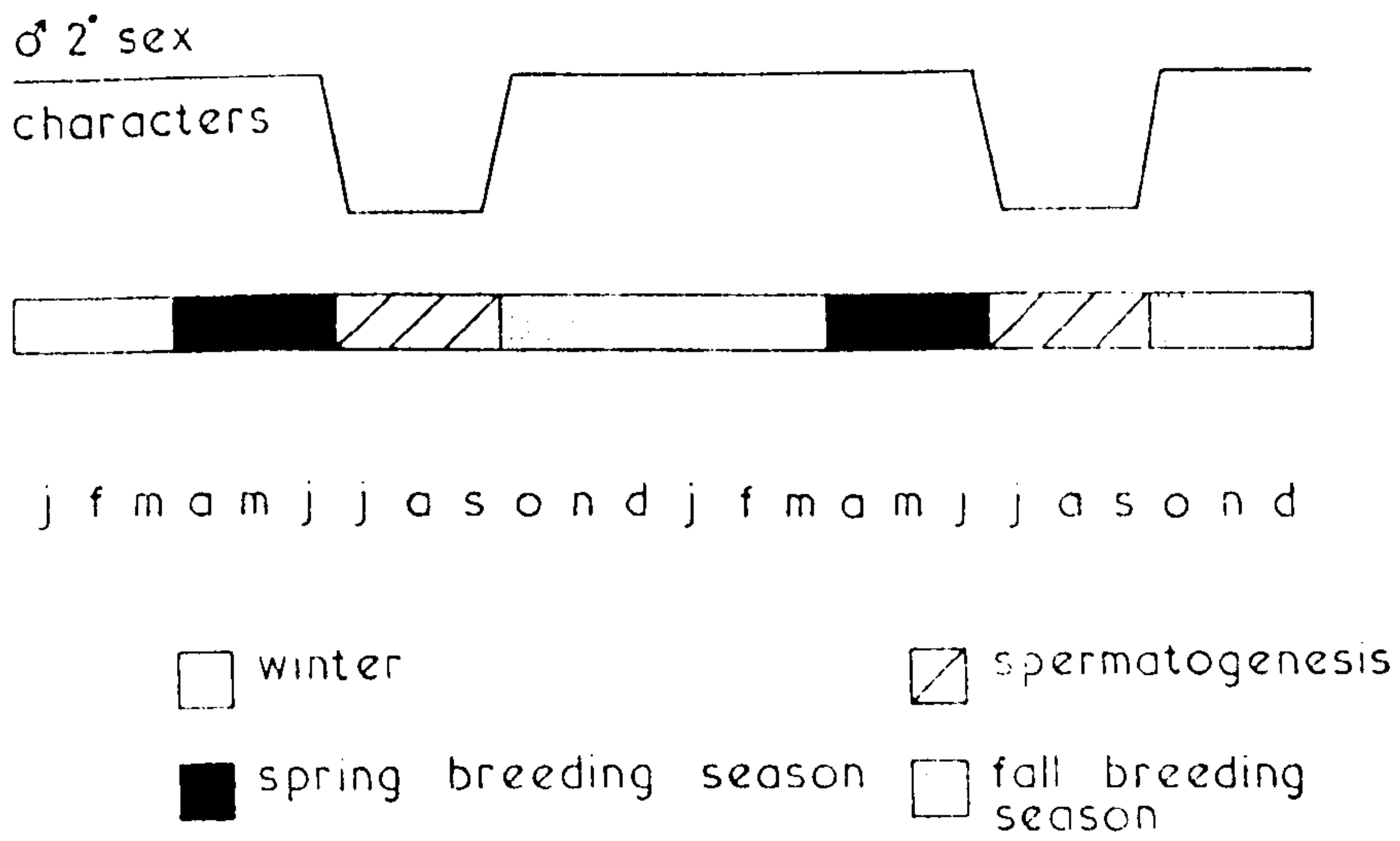


Figure 3.1 Diagrammatic summary of the annual cycles of spermatogenesis and development of secondary sexual characteristics in male red-spotted newts. Data taken from Adams (1940).

(Reese 1917) and can entrain to an artificial photoperiodic schedule even when blinded. The pineal organ, an outgrowth of the brain, acts as an accessory photosensitive structure (Demian and Taylor 1977). Vision is also important in homing behaviour (Hershey and Forester 1980), which also implies an ability to form long term spatial maps of the environment. The most direct evidence for a role of vision in a sexual context is the work of Evans (1960), who found that males can discriminate between large and small females on the basis of visual cues.

Olfaction is also important in feeding and homing behaviours (reference as above). There is good evidence that glands on the male's head and in his cloaca are used during courtship to stimulate the female (discussed in Chapter 3.2), and Evans (1960) provides some evidence for sex discrimination on the basis of olfactory cues.

The brighter colouration of the male newt suggests both an influence of sexual selection and a capacity for colour vision. However, this colouration may not be sexual, or even intraspecific, in function. It may, for instance, be aposematic, for like the eft, the adult newt is endowed with poison-secreting glands. The greater activity of the male, perhaps resulting in a greater risk of being detected by a predator, may be sufficient to account for his greater adornment.

3.2 The Sexual Behaviour of the Red-Spotted Newt: A Review

Despite relatively intensive ecological studies, few workers have considered the sexual behaviour of the red-spotted newt in any detail. One of the earliest accounts in the literature is that of Pike (1886). He described how the male gyrates in front of the female before seizing her around the neck with his powerful hindlimbs. Pike also described how the resulting period of amplexus may last for many hours, but stated, quite

erroneously, that....."the milt and ova pass simultaneously" (p. 19).

Spallanzani (1780) had demonstrated internal fertilization in the related genus *Triturus* a century earlier, and a similar mode of fertilization exists in *Notophthalmus*.

Zeller (1890) also described how the male captures the female around the neck, and went on to provide some details of the amplexant male's behaviour. In particular, Zeller noted that the male vibrates his tail alongside the body of the female.

Jordan (1891) observed that the male newt's courtship is divided into three parts: 1) gyration in front of the female, 2) amplexus and 3) dismounting and spermatophore transfer behaviour. He confirmed Zeller's observation of tail vibration during amplexus and described how a pair in amplexus thrash about in the water just before the male dismounts, the latter....."quivering with excitement" (p. 269). Jordan also gave some details of spermatophore transfer behaviour, and calculated the probability of successful spermatophore pick up as about 20 per cent. Similar observations were made by Gage (1891).

Further information on the behaviour of the amplexant male was provided by Hilton (1902). He described how the male rubs and presses his cheeks over the female's snout. Hilton examined the cheeks of the male histologically and found a set of glands behind each eye, the genial glands. In a simple and poorly reported experiment, Rogoff (1927) found that the application of the glands to the nostrils of a female causes her to follow the male closely during spermatophore transfer behaviour.

Pope (1924) described much of the repertoire of the amplexant male, but his account is brief and lacks quantitative data. However, one important observation of his is that, in the field, a single female may be the focus

attention of several males at the same time. Similarly, D.E. Gill (personal communication) describes how males 'grapple' over females.

The first worker to realize that the sexual behaviour of *Notophthalmus* consists of two types was Humphries (1955). He found that a male will not attempt amplexus in the presence of an initially responsive female; his responsive females had been implanted with homologous pituitary glands. Instead, the male enters spermatophore transfer behaviour after a brief period of gyration. Humphries also gave some details of the behaviour performed during amplexus and suggested that an amplexus encounter can be divided into a number of temporally consecutive phases.

The most recent and most complete account of the sexual behaviour of this species is provided by Arnold (1972, 1977). He has confirmed the bimodal structure of the behaviour and has devised an extensive ethogram of the actions of the male and, to a lesser extent, of the female. He has also provided a detailed verbal description of the temporal patterning of the behaviour, especially for amplexus.

Table 3.1 is a list of the various actions that comprise the sexual behaviour of the red-spotted newt. It shows which authors described which actions, and places the observations of the present study in an historical perspective.

3.3 General Methods

Origins of Animals

All of the red-spotted newts used in the experiments reported in this Chapter and in Chapter 4 were collected as they migrated to a breeding site in Wilson County, Tennessee, USA.

| Action | Pike 1886 | Zeller 1890 | Jordan 1891 | Gage 1891 | Hilton 1902 | Pope 1924 | Humphries 1955 | Arnold 1972 | Verrell 1983 |
|--------------------------|--------------|----------------|----------------|--------------|----------------|--------------|-------------------|----------------|-----------------|
| Alert posture | | | | | | | ✓ | | ✓ |
| Gyration | ✓ | | ✓ | ✓ | | | ✓ | ✓ | ✓ |
| Guff | | | | | | | | | ✓ |
| Creep | | ✓ | ✓ | | ✓ | ✓ | ✓ | ✓ | ✓ |
| Tail touch | ✓ | | ✓ | | | ✓ | ✓ | ✓ | ✓ |
| Deposition | | ✓ | ✓ | | ✓ | | ✓ | ✓ | ✓ |
| Creep on | | | ✓ | | ✓ | | ✓ | ✓ | ✓ |
| Pivot | | | | | | | | ✓ | ✓ |
| Pick up | | | ✓ | | ✓ | | ✓ | | ✓ |
| Clasping | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Cheek rub | | | | | ✓ | ✓ | ✓ | ✓ | ✓ |
| Forelimb rub | | | | | | | | ✓ | ✓ |
| Head turn | | | | | ✓ | ✓ | ✓ | ✓ | ✓ |
| Tail turn | | | ✓ | | | | | ✓ | ✓ |
| Tail vibration | ✓ | ✓ | ✓ | | ✓ | ✓ | ✓ | ✓ | ✓ |
| Phase 1 | | | ✓ | | ✓ | ✓ | ✓ | ✓ | ✓ |
| Phase 2 | | | ✓ | | ✓ | ✓ | ✓ | ✓ | ✓ |
| Phase 3 | | | | | | | | ✓ | ✓ |
| Dismount | | ✓ | ✓ | | ✓ | | ✓ | ✓ | ✓ |
| Tail lift | | | ✓ | | | ✓ | ✓ | | ✓ |
| Female rejection posture | | | | | | | | ✓ | |

Table 3.1 The actions that comprise the sexual behaviour of the red-spotted newt, showing which authors described which actions.

Keeping of Animals

Newts were received in the winters of 1979-1980, 1980-1981 and 1981-1982. They were airfreighted from Chicago, Illinois, USA in plastic boxes containing wet leaves, these boxes packed inside an insulating polystyrene container. Upon receipt, the newts were segregated according to sex and housed in the same way as described in Chapter 2.3 for smooth newts (see also Verrell 1982b).

Experimental Procedure

The general experimental procedure employed for *Notophthalmus* closely resembled that described in Chapter 2.3 for smooth newts. Specific methods are described in the individual sections of this Chapter and Chapter 4.

3.4 The Sexual Behaviour of the Red-Spotted Newt in Encounters between Single Males and Females

In this section, the sexual behaviour of the red-spotted newt in male-female dyads is qualitatively and, where possible, quantitatively described. A preliminary report of these findings has been published (Verrell 1982a).

3.4.1 A Description of Sexual Behaviour

Method

All observations were made in an observation tank measuring 61 x 30 x 30 cm. Behaviour was recorded as an audiovisual commentary on videotape and, as explained later, the time-lapse tape speed facility was used occasionally. As many encounters between pairs of newts were observed as possible, although each newt was used as seldom as possible. The following account is based on 226 encounters, involving 200 males and 120 females.

Observations

The male and female must come together before any sexual behaviour can occur. The majority of contacts between a pair are accidental, the animals encountering one another as they move around the tank. Sexual behaviour is most likely to follow a 'directed approach' made by the male to the female. Such an approach can easily be distinguished from an accidental contact, as the male typically adopts an 'alert posture', with his body raised from the substrate supported by his hindlimbs and tail. In this position, he seems to 'scan' the vicinity for the female. Precht1 (1951) and Halliday (1974) describe a similar posture in the related genus *Triturus*. The rate of approach of the male is related to the distance separating him from the female; as he gets closer to her, he moves more slowly. The subsequent behaviour of the male depends on that of the female.

Behaviour when the Female is Initially Responsive

A female who stays close to the male when approached is said to be initially responsive (Arnold 1972). When close to the female, the male nudges her with his snout and begins to make rapid movements of the floor of his mouth. Such buccopharyngeal pumping indicates that the male is sniffing the female; she may also nudge and sniff him. After a few seconds, the male's body is thrown into lateral, serpentine undulations, which begin in the pectoral region and pass down to the end of his tail. His hindlimbs may lift from the substrate and swing from side to side as the vigour of these undulations increases. Arnold (1972) has called this behaviour 'hula display', as the male's contortions are reminiscent of those of a Hawaiian dancer.

The partners gradually shift position until they become more or less perpendicular to one another, head to head. The male's body is held straight, although his tail may flex towards the female in a way similar

to that of a male smooth newt performing 'wave' display (Halliday 1974). The male's cloaca is everted throughout hula display, revealing its pink papillae and pale glands. Hula display is depicted in Figure 3.2.



Figure 3.2 Hula display in the red-spotted newt, viewed from the side. The male, on the left, approaches the female (A) and begins to undulate his body and tail (B). The female edges closer to the male (C), and he turns away to creep (D and E).

The transition from hula display to spermatophore transfer behaviour is a gradual one. Continuing to undulate, the male turns so that he faces

away from the female. As he turns, he releases a stream of air bubbles from his mouth, an action known as 'guffing' (Spurway and Haldane 1953). Spermatophore transfer behaviour begins when the male has completed his turn. His subsequent behaviour closely resembles that of newts of the genus *Triturus*, and I have borrowed freely from the terminology of Halliday (1977a) developed for the latter.

Spermatophore transfer behaviour is shown in Figure 3.3. When fully turned, the male begins to 'creep'. He flexes his tail at 90° to his body and holds it parallel to the substrate. Moving more or less in a straight line, he then shuffles forwards about 10 cm. The female follows,

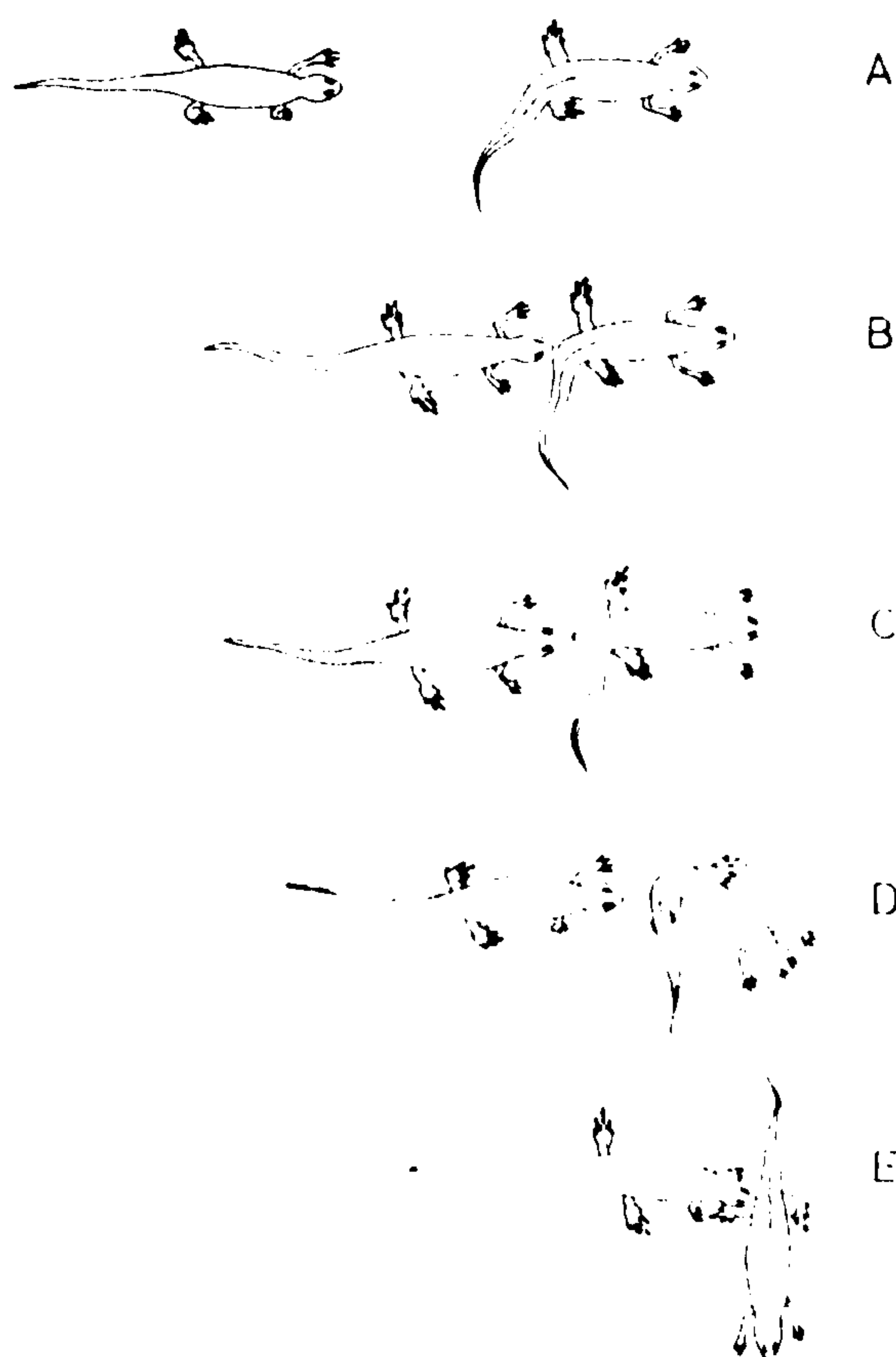


Figure 3.3 Spermatophore transfer behaviour in the red-spotted newt, viewed from above. The male, on the right, creeps (A) and is followed by the female, who nudges at his tail (B). He then deposits a spermatophore (C), and creeps-on one body length (D). He then brakes (E).

repeatedly nudging at his everted cloaca with her snout. The conspicuousness of this area is enhanced by the visual stimuli of its papillae and glands, and by lateral movements of the sacrum. Odours from the dorsal glands in the cloaca (Sever 1981) may also help orient the female. The male then stops moving and the female literally bumps into his tail. The male's undulations decrease in vigour, and he lowers his cloaca and presses its papillae to the substrate. A few seconds later, he lifts his cloaca, which opens fully, and the spermatophore appears, a white sperm-filled cap surmounting a gelatinous stalk which is attached to the substrate, in front of the female's snout. The male then moves forwards, away from the spermatophore ('creep-on') and stops after a few centimetres; he also resumes full body and tail undulation. The female follows, nudges the male's tail, and he moves forwards a little more. He then pivots through 90° so as to block the female's path. As he pivots, his tail swings back to a position straight behind his body ('brake').

In moving forwards from the site of deposition to the position adopted at brake, the male creeps-on about one snout-vent body length. Provided she follows the male closely, the female should end with her snout pressed to his tail and her cloaca in the close vicinity of the spermatophore. The process of attachment of the latter to the female's cloaca is poorly understood. It appears that pick up is made more likely by 1) extension of the female's cloaca, 2) small anteroposterior and lateral movements of her body and 3) the rim of cornified cells around her extended cloaca. Only the white sperm cap is taken up by the female, the gelatinous stalk to which it was attached remaining fixed to the substrate.

The pair may remain in the brake position for some time; indeed, the male will hold it even if the female moves away. If she does move away, for example, to surface for air, she may or may not return to the male. If she continues to nudge at his tail, the male may creep again, thus

initiating another sequence of spermatophore transfer behaviour. Up to five such sequences may occur in a single encounter.

Behaviour when the Female is Initially Unresponsive

A female may be considered initially unresponsive if she moves away when approached by the male (Arnold 1972). The male attempts to clasp such a female around the neck with his hindlimbs. From a stationary start, usually behind or to one side of the female, the male springs from the substrate, propelled by a thrust from his hindlimbs and tail. Rising a few centimetres in the water, the anterior part of his body is thrown up and back, his forelimbs limp by his sides. His hindlimbs gape open like a pair of tongs, ready to close about the body of the female.

Not all attempts at capture are successful (26.7% are 'misses'). Actual captures fall into one of several categories. Those in which the partners are back-to-front always end in the female either escaping or being released; the male is unable to turn whilst retaining his grip on the female. Escape or release also occurs when a female is clasped around her tail. If the male captures the female around her body, he shuffles forwards until he is positioned correctly. Often, the male succeeds in a neck-clasp at first attempt; his forelimbs are not used to clasp the female, in contrast to some other urodeles (Arnold 1977). Sometimes, an apparently successful capture terminates soon after its initiation, with the male releasing the female. Arnold (1972) has observed a 'head down' posture shown by captured females which leads to their release. I have not observed this posture during heterosexual encounters, but have seen it in male-male encounters, when it does lead to the release of the clasped male.

With the male locked around the female's neck (see Figure 3.4), the pair are said to be in amplexus. Arnold (1972) has described five specific actions performed by a male in amplexus:



Figure 3.4 The posture adopted by a pair of red-spotted newts during amplexus. The male's cheek is pressed to the female's snout, and his tail is flexed to one side of her body. Inset: the three genial pits behind the eye of the male.

1. Cheek rubbing: throughout amplexus, the male rubs the genial glands on each of his cheeks over the female's snout (Figure 3.5A).
2. Forelimb rubbing: the male lifts his forelimb nearest the female's snout and rubs its inner surface over her nostrils. When I histologically examined male forelimbs, I saw no specialized glandular tissue like that found on male cheeks (Figure 3.5B).
3. Head turning: the male continuously changes the side to which his head is flexed, relative to the female's head, which results in each set of genial glands being applied to her snout. Even when not being rubbed over the female's snout, the male's glands are pressed to it (Figure 3.5C).
4. Tail turning: the male jerks his tail from one side of the female's body; between each jerk, his tail is held parallel to her body (Figure 3.5D).
5. Bouts of tail vibration: when held parallel, the male vibrates the tip of his tail laterally. By releasing a small amount of carbon

particle suspension near the male's cloaca, it can be seen that these vibrations set up water currents which move anteriorly towards the female's head. The vibrations occur in bouts of about 1 second duration, with an interbout interval of variable duration (Figure 3.5E).

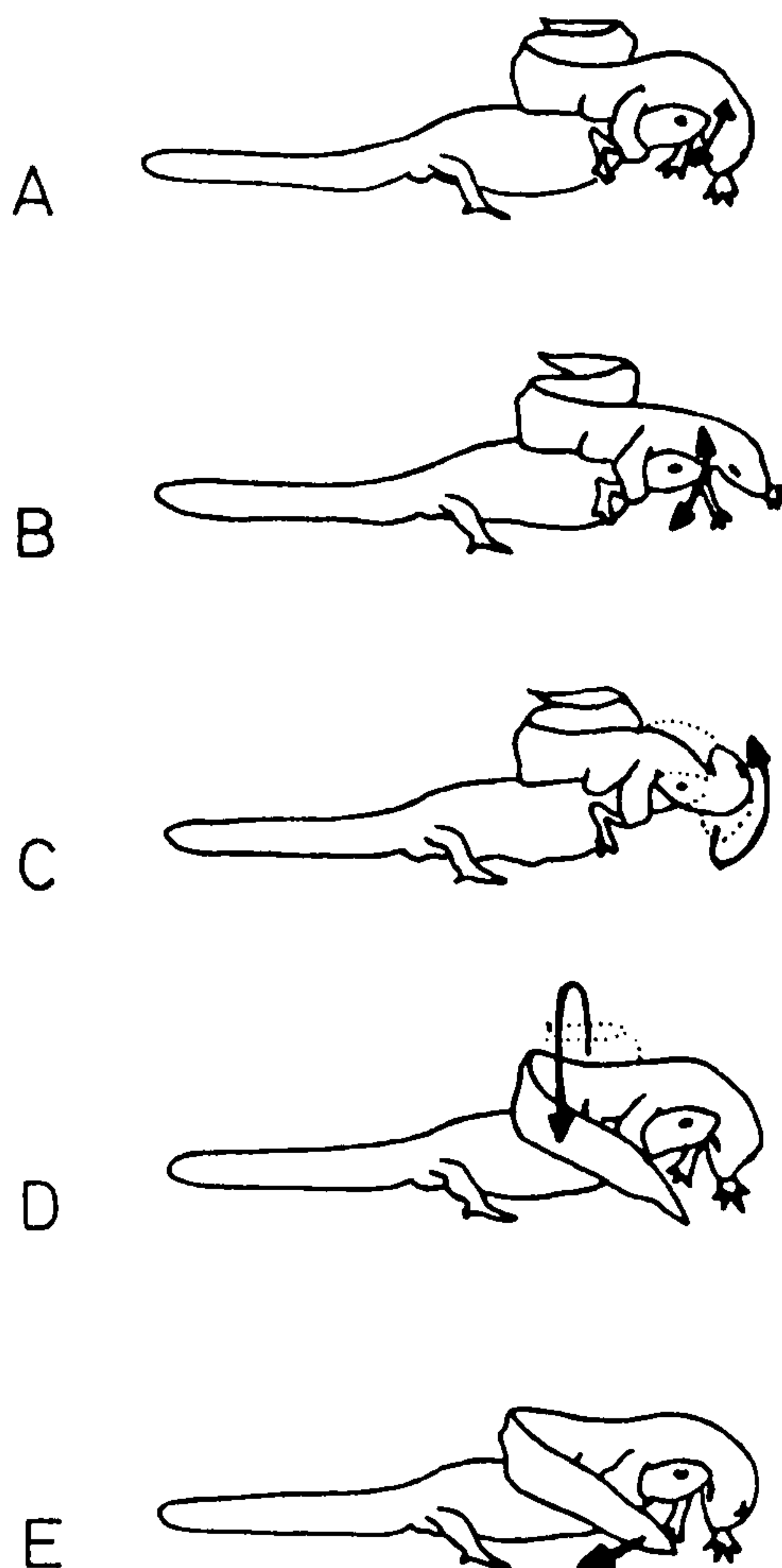


Figure 3.5 The actions performed by the male during amplexus. A. cheek rubbing; B. forelimb rubbing; C. head turning; D. tail turning; E. bouts of tail vibration.

Analysis of the temporal patterning of amplexus

Ten complete amplexus encounters were observed and all five of the actions described above were recorded using the 'all occurrence sequence sampling' technique of Lehner (1979). Each of these 10 encounters was then divided into a series of consecutive 5 minute time blocks, and the

number of each male action per block was extracted from videotape records (because both types of rubbing occur in a predictable sequence of "limb, cheek..." etc, only the score for cheek rubbing is considered). Figure 3.6 shows such a record for one of these encounters.

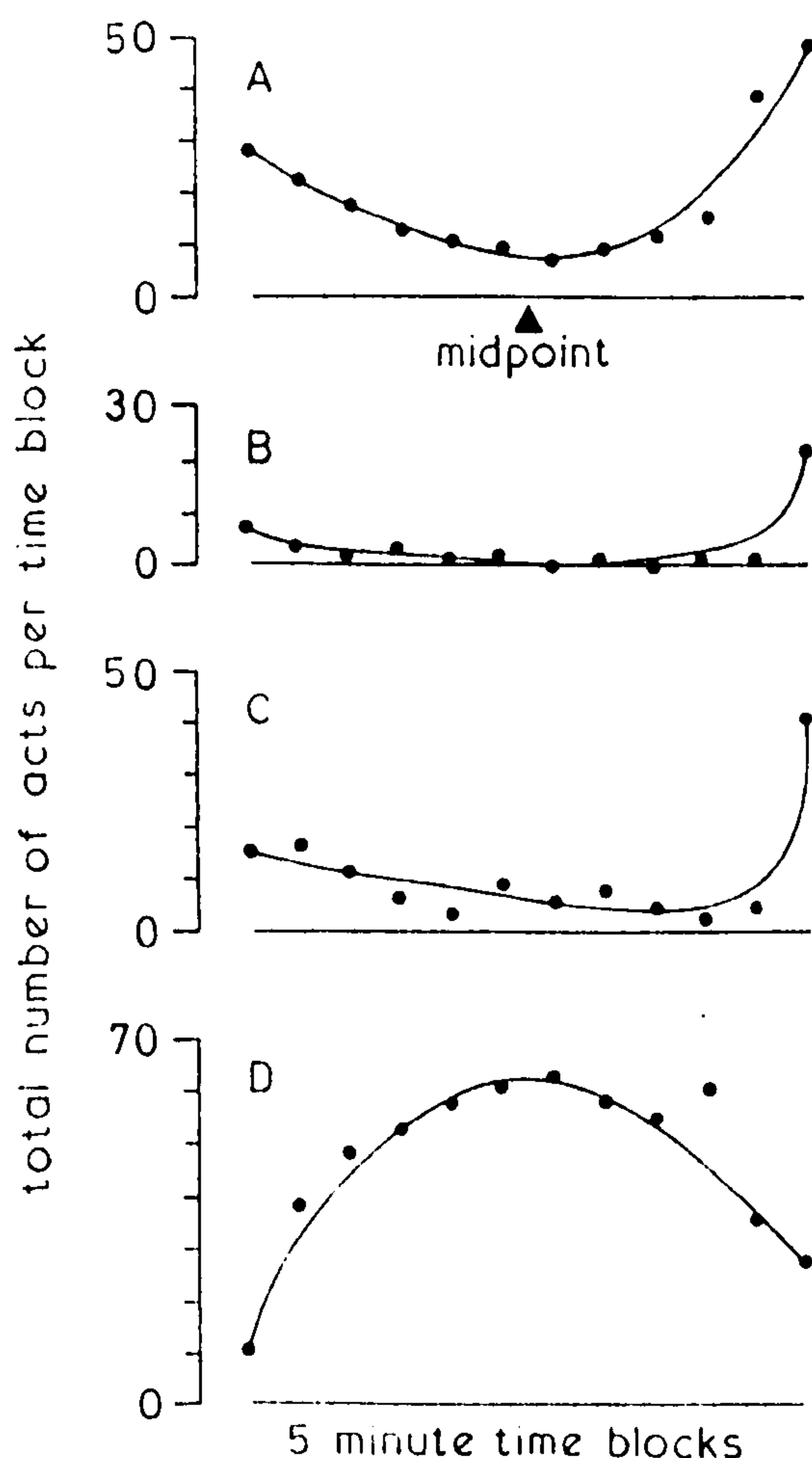


Figure 3.6 The temporal patterning of male display behaviour for a single amplexus encounter. A. cheek and forelimb rubbing; B. head turning; C. tail turning; D. bouts of tail vibration.

A further 35 encounters were filmed using the time-lapse tape speed facility on the videotape recorder (recording interval 0.18 seconds as against 0.02 seconds for normal speed). The records of these 35 encounters were then analyzed as described above. Only data for five encounters are shown graphically in Figure 3.7, these five selected at

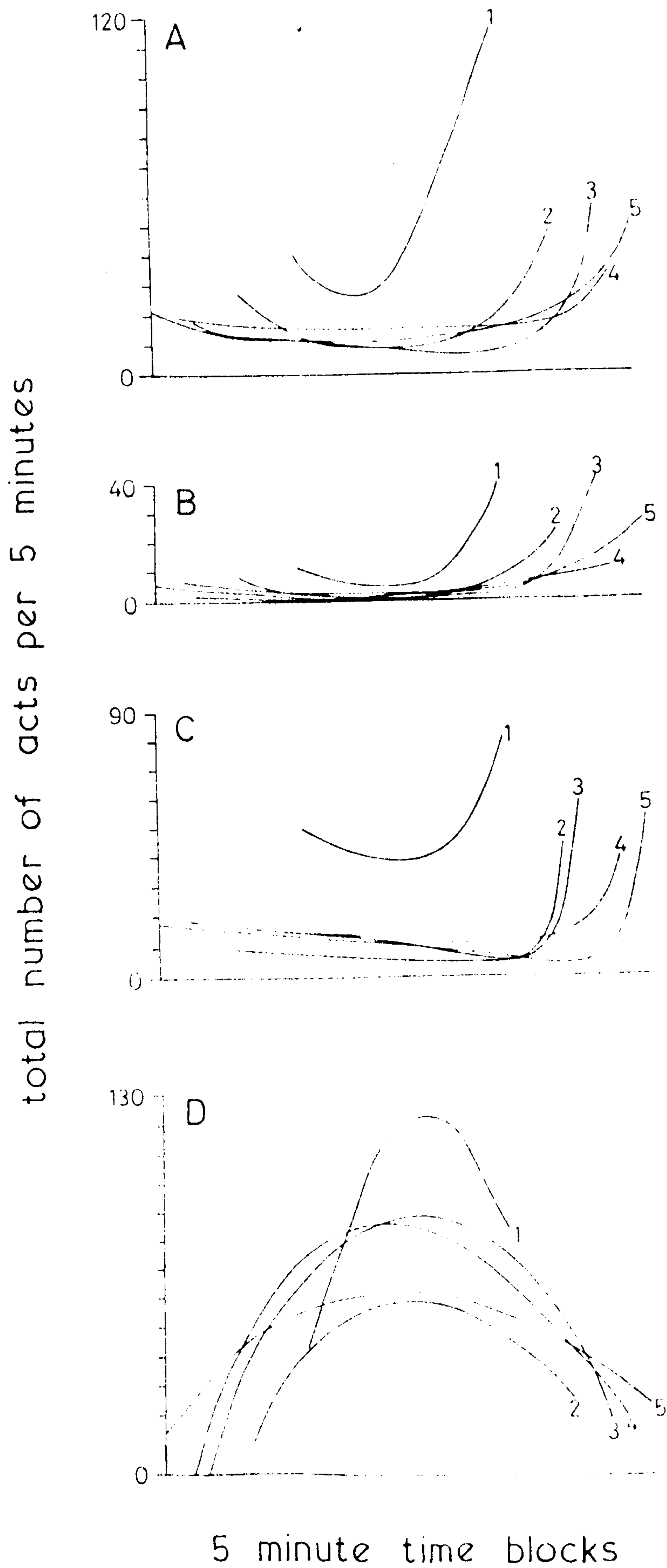


Figure 3.7 The temporal patterning of male display behaviour for five amplexus encounters of different durations. Axes as in Figure 3.6.

random from all of those available. As each of these were of different durations, the curves have been plotted such that the midpoints of all the curves coincide.

After the capture of the female by the male, the pair thrash about in the water for a while, the female occasionally becoming freed. This soon gives way to the first phase of amplexus, during which the male decreases the rate at which he turns his head and, to a lesser extent, his tail. He also performs less cheek and forelimb rubbing, but the number of bouts of tail vibration performed increases.

The male's activity remains more or less at a constant pitch for a time and then, quite suddenly, head and tail turning and cheek and forelimb rubbing increase in frequency whilst tail vibration decreases. Arnold (1972) states that "the male moves into continuous activity" (pages 255, 256); his description of the male's subsequent behaviour closely resembles mine, and constitutes the second phase of amplexus.

When the male turns his head, he performs several rapid, lateral swings of his body before allowing it to settle on the opposite side. The repeated sequence 'forelimb rub, cheek rub, tail vibration, head front, body swing, head and tail turn...' becomes apparent. Between swings, the male's head and tail lie on the same side of the female. The swings may be so vigorous that the pair thrash about in the water, sometimes rising almost to the surface. However, neither member of an amplexant pair has ever been observed to breathe.

This second phase gradually gives way to the third phase of amplexus. The male turns his head and tail more slowly, and no longer performs cheek and forelimb rubbing. Tail vibration is maintained. Activity becomes more and more slow until the male finally straightens his body, releases

his hold on the female and dismounts over her head, guffing as he does so. The mean duration of amplexus (\pm SEM) was 102.3 ± 3.5 minute (N = 73), with a range of 40-201 minutes.

The female is then free to move away from the male, perhaps to breathe, or remain with him. If she stays and nudges his tail, he will creep and thus initiate spermatophore transfer behaviour. This is qualitatively similar to that which follows hula display (Figure 3.3).

Although the female is an active participant in hula display, she often remains motionless during amplexus. Some females, however, slowly lift their tails from the substrate, holding them at an angle to the rest of the body (see Figure 3.4). Jordan (1891), Pope (1924) and Humphries (1955) also observed tail lifting. However, its significance, if any, is unknown.

Interactions between the male's display actions during amplexus encounters

To obtain further information on the nature of the amplexant male's behaviour, the videotape records for the 45 encounters observed were re analyzed, and a number of 'courtship variables' calculated for each of the male's five display actions. These courtship variables, together with their definitions, are:

1. Duration of amplexus - from the time of capture to dismount.
2. Total number scores - the total number of each act performed over the duration of amplexus for a) cheek rub, b) forelimb rub, c) head turn, d) tail turn and e) tail vibration.
3. Overall rate scores - the total number of each act divided by the duration of amplexus for a) to e) above.

4. Mid rate scores - the number of each act performed during the middle 5 minutes of amplexus for a) to e) above.
5. End rate scores - the number of each act performed during the last 5 minutes of amplexus for a) to e) above.

In Table 3.2, the relationships between these scores are presented in a Spearman's rank-order correlation matrix (see Siegel 1955, Nie et al. 1975). Out of the 231 possible correlations in this Table, 85 (36.8 per cent) are significant at the 0.05 level or better. Of these, only eight (9.4 per cent) are negative. As can be seen, the total numbers of all five male display actions are positively correlated with the duration of amplexus, but the overall rates of all actions except tail vibration are negatively correlated with duration. This interesting finding is discussed later in this section.

By way of a summary, the sexual behaviour of the red-spotted newt is depicted as a kinematic graph in Figure 3.8. The flow diagram in Figure 3.9 quantifies the relationships between different parts of the courtship encounter. Arrow width is proportional to the probability of one part leading to another.

The Success of Sexual Behaviour

Hula courtships

A total of 95 encounters consisting only of hula display were observed. In 36 (37.9 per cent), the female fled from the male as he displayed to her. Of the other 59 in which the female stayed with the male, only 18 (30.5 per cent) resulted in the transfer of at least one spermatophore. The mean number of spermatophores deposited per hula encounter (\pm SEM) was 2.3 ± 0.12 . Table 3.3 presents data on the frequency of encounters of different lengths

| Duration | Total number | | | | | | Overall rate | | | | | | Mid rate | | | | End rate | | | | |
|----------|--------------|----------|-----------|-----------|------------|--|--------------|----------|-----------|-----------|------------|-----------|----------|-----------|-----------|------------|-----------|----------|-----------|-----------|------------|
| | Check rub | Limb rub | Head turn | Tail turn | Tail vibr. | | Check rub | Limb rub | Head turn | Tail turn | Tail vibr. | Check rub | Limb rub | Head turn | Tail turn | Tail vibr. | Check rub | Limb rub | Head turn | Tail turn | Tail vibr. |
| 1 | 0.49 | 0.49 | 0.30 | 0.33 | 0.70 | | -0.50 | -0.50 | -0.40 | -0.36 | | | | | | -0.30 | | | | | |
| 2 | | 0.99 | 0.40 | 0.50 | 0.55 | | 0.40 | 0.40 | | | | 0.50 | 0.55 | | | | | | | | |
| 3 | | | 0.40 | 0.46 | 0.57 | | 0.40 | 0.40 | | | | 0.50 | 0.54 | | | | | 0.25 | | | |
| 4 | | | | 0.37 | 0.30 | | | | 0.65 | | | | | 0.33 | | | | | 0.44 | 0.38 | |
| 5 | | | | | 0.40 | | | | | 0.70 | 0.26 | | | | 0.50 | | | | | 0.39 | |
| 6 | | | | | | | -0.26 | | -0.37 | | 0.50 | | | | | | | | | | 0.28 |
| 7 | | | | | | | | 0.97 | 0.37 | 0.38 | 0.28 | 0.60 | 0.60 | | 0.27 | 0.26 | 0.25 | 0.30 | | | |
| 8 | | | | | | | | | 0.38 | 0.40 | 0.30 | 0.60 | 0.60 | | 0.29 | 0.34 | 0.25 | 0.32 | | | |
| 9 | | | | | | | | | | 0.31 | | 0.25 | | 0.42 | | | 0.42 | 0.38 | | | |
| 10 | | | | | | | | | | | 0.30 | | | | 0.60 | 0.25 | | | 0.28 | | |
| 11 | | | | | | | | | | | | 0.26 | 0.25 | | | 0.75 | | | | | 0.50 |
| 12 | | | | | | | | | | | | | 0.97 | 0.44 | 0.40 | 0.25 | | | | | 0.30 |
| 13 | | | | | | | | | | | | | | 0.40 | 0.40 | | | | | | 0.30 |
| 14 | | | | | | | | | | | | | | | 0.26 | | | | | | |
| 15 | | | | | | | | | | | | | | | | | | | | | |
| 16 | | | | | | | | | | | | | | | | | | | | | -0.61 |
| 17 | | | | | | | | | | | | | | | | | 0.96 | | | | |
| 18 | | | | | | | | | | | | | | | | | | | | | |
| 19 | | | | | | | | | | | | | | | | | | | | 0.58 | |
| 20 | | | | | | | | | | | | | | | | | | | | | |
| 21 | | | | | | | | | | | | | | | | | | | | | |

Table 3.2 Spearman's rank-order correlation matrix between the duration of amplexus and a number of male display scores.
 $r_s > 0.25$, $P < 0.05$; $r_s > 0.37$, $P < 0.01$; $r_s > 0.44$, $P < 0.001$.

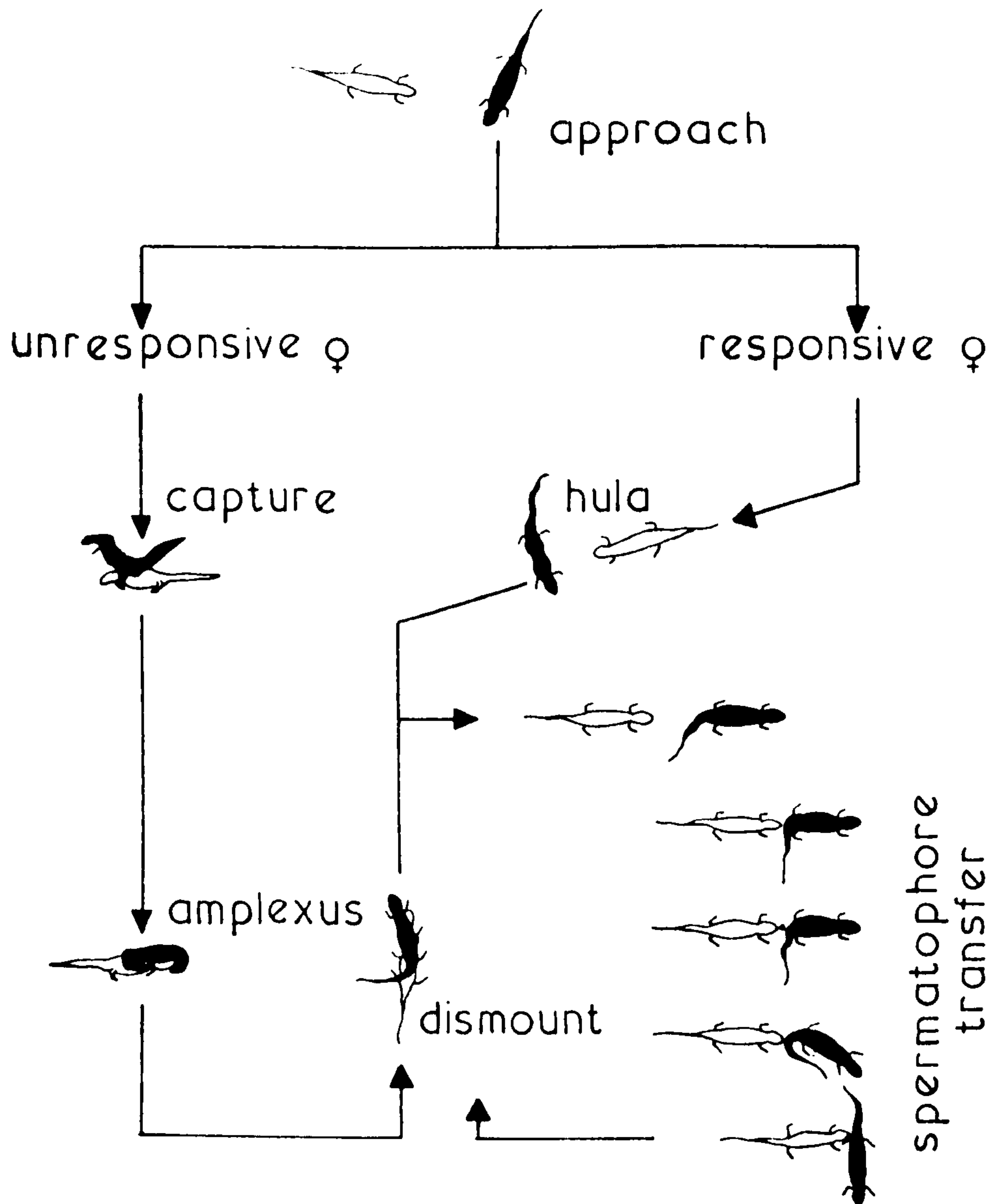


Figure 3.8 Diagrammatic summary of the two modes of sexual behaviour sequence in the red-spotted newt. The male is in black.

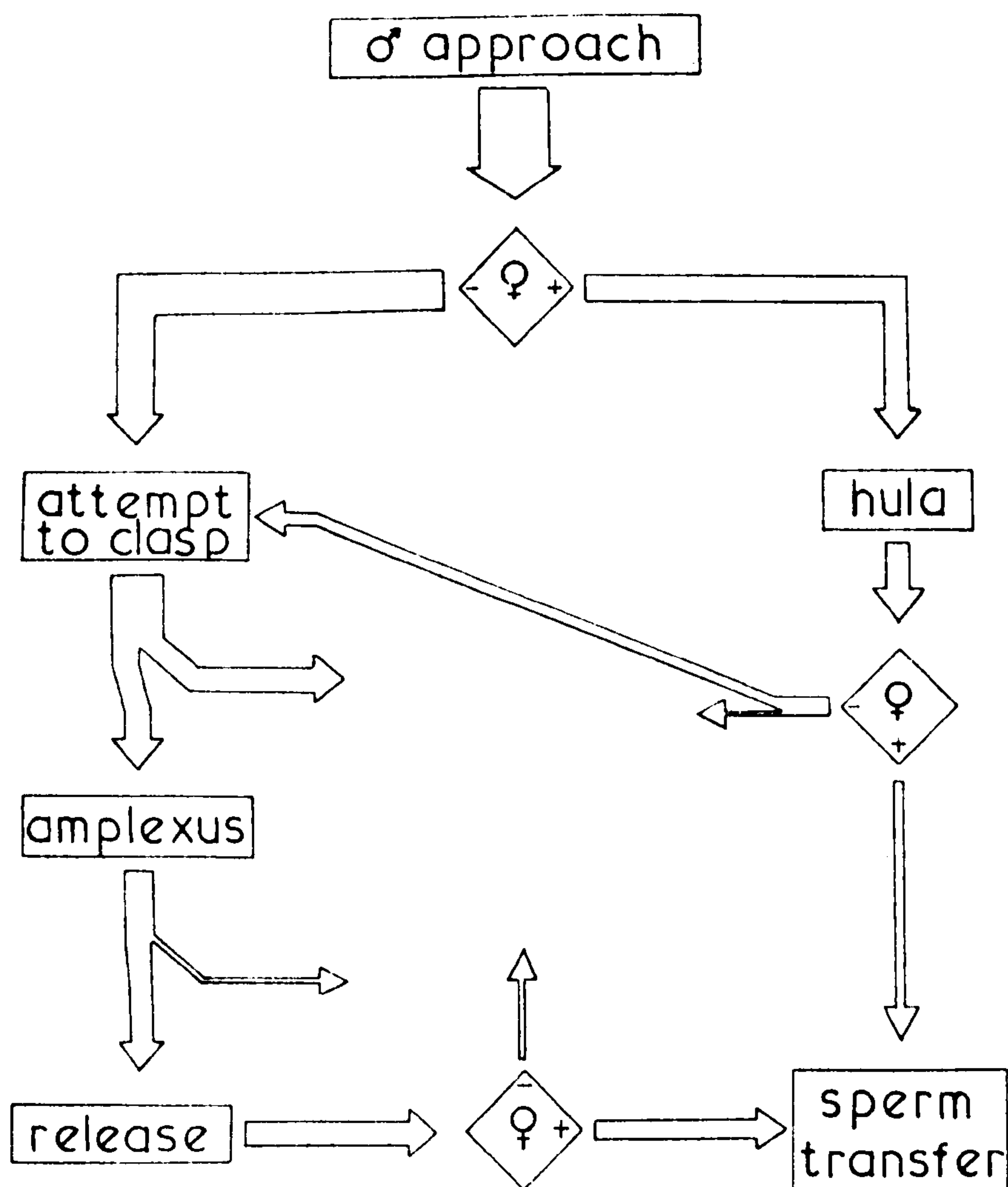


Figure 3.9 Flow diagram showing the frequency with which pairs of red-spotted newts proceed from one stage of a sequence to the next. The width of the arrows is proportional to the frequency of transition. Diamonds represent decision boxes: - is female moving away, + is female nearby.

| Number of depositions per encounter | N | Number of successful pick ups | | | | |
|-------------------------------------|----|-------------------------------|-------------|------------|-----|-----|
| | | 1st | 2nd | 3rd | 4th | 5th |
| 1 | 12 | 2 (17%) | | | | |
| 2 | 21 | 5 (24%) | 3 (14%) | | | |
| 3 | 17 | 6 (35%) | 4 (23%) | 5 (29%) | | |
| 4 | 7 | 4 | 3 | 2 | 2 | |
| 5 | 2 | 0 | 0 | 1 | 2 | 1 |
| Total | | 17 (29%) | 10 (21%) | 8 (31%) | | |

Percentages calculated only when N ≥ 10.

Table 3.3 The rate at which spermatophores are picked up by females in relation to the order in which they are deposited: Hula courtships.

in terms of the number of spermatophores deposited and the pick up success of these spermatophores. The probability of pick up was more or less constant for any spermatophore regardless of its position in an encounter.

Amplexus courtships

Of 206 attempted captures observed, 55 (26.7) resulted in the male failing to clasp the female, who moved too rapidly or escaped during the initial stages of amplexus. Successful amplexus leading to dismount was the result in 131 (63.6 per cent) capture attempts. Of these, 16 (12.2 per cent) resulted in the female moving away when released and 72 (55 per cent) in the transfer of at least one spermatophore to the female.

The mean number of spermatophores deposited per amplexus courtship (\pm SEM) was 2.34 ± 0.08 , and as Table 3.4 shows, spermatophores deposited earlier in an encounter enjoyed slightly greater pick up success than those deposited later.

None of the courtship variables discussed earlier were significantly correlated with either the number of spermatophores deposited or the number picked up. In order to determine if some combination of variables might be important, I summed the total number of forelimb and cheek rubs and bouts of tail vibration for each of 45 encounters. This composite score, termed 'number of acts', is a gross measure of the total amount of olfactory and tactile stimulation received by the female. Figure 3.10 shows the relationship between number of acts and number of spermatophores deposited ($r_s = 0.66$, $P < 0.001$) and Figure 3.11 shows that between number of acts and number of spermatophores picked up ($r_s = 0.45$, $P < 0.01$). Thus, although the score 'number of acts' fails to account for much of the variance in spermatophore-related behaviour, both deposition and pick up rate increase as more stimulation is given to the female.

| Number of depositions per encounter | N | Number of successful pick ups | | | | |
|-------------------------------------|----|-------------------------------|-------------|-------------|------------|-----|
| | | 1st | 2nd | 3rd | 4th | 5th |
| 1 | 20 | 9 (45%) | | | | |
| 2 | 43 | 29 (67%) | 22 (51%) | | | |
| 3 | 39 | 26 (66%) | 24 (61%) | 19 (49%) | | |
| 4 | 10 | 7 (70%) | 8 (80%) | 7 (70%) | 6 (60%) | |
| 5 | 3 | 1 | 3 | 0 | 3 | 1 |
| Total | | 72 (63%) | 57 (60%) | 26 (50%) | | |

Percentages calculated only when N > 10.

Table 3.4 The rate at which spermatophores are picked up by females in relation to the order in which they are deposited: Amplexus courtships.

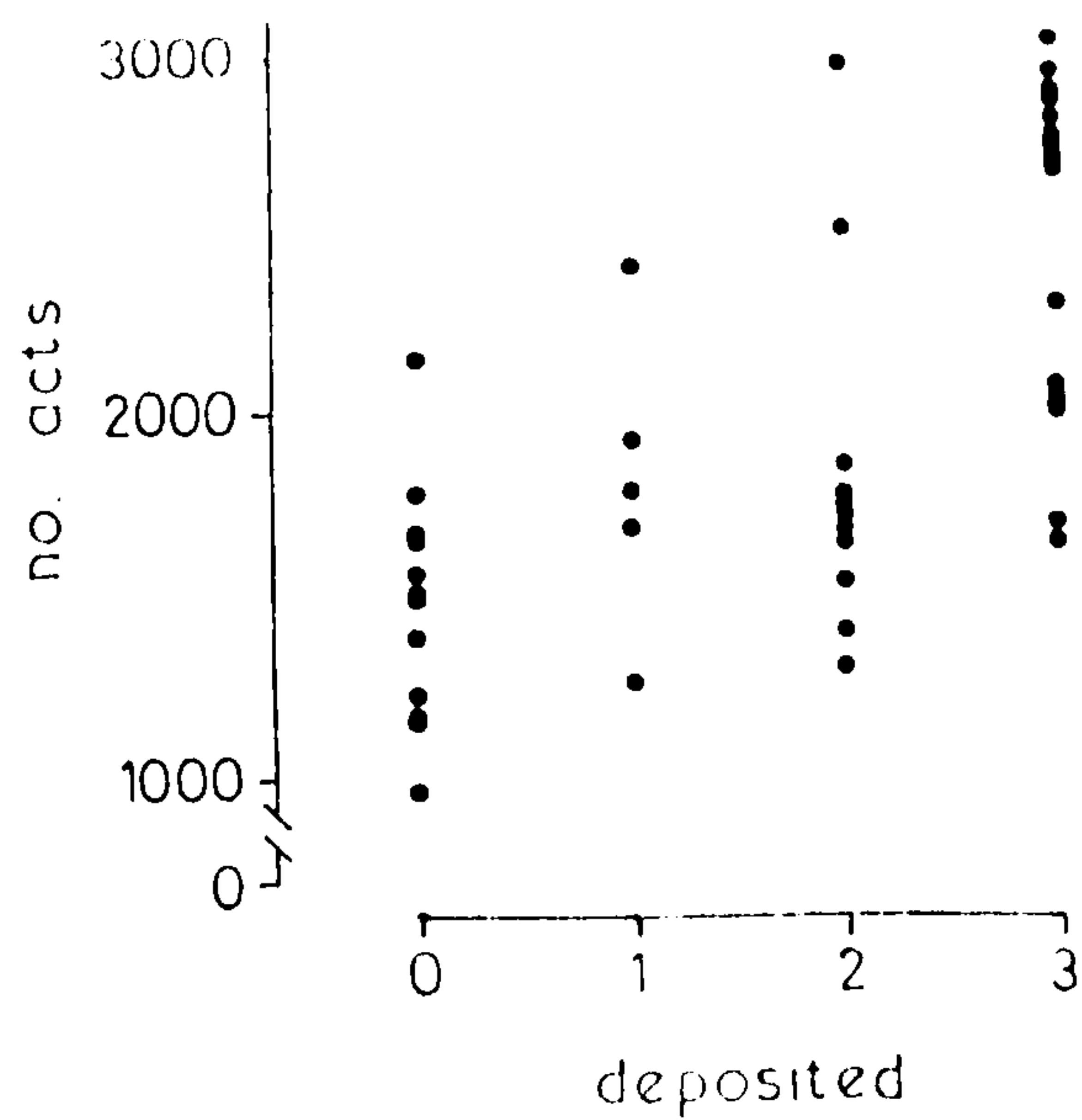


Figure 3.10 The relationship between a composite score of number of cheek rubs plus number of forelimb rubs plus number of bouts of tail vibration, and the number of spermatoophores deposited during amplexus encounters.

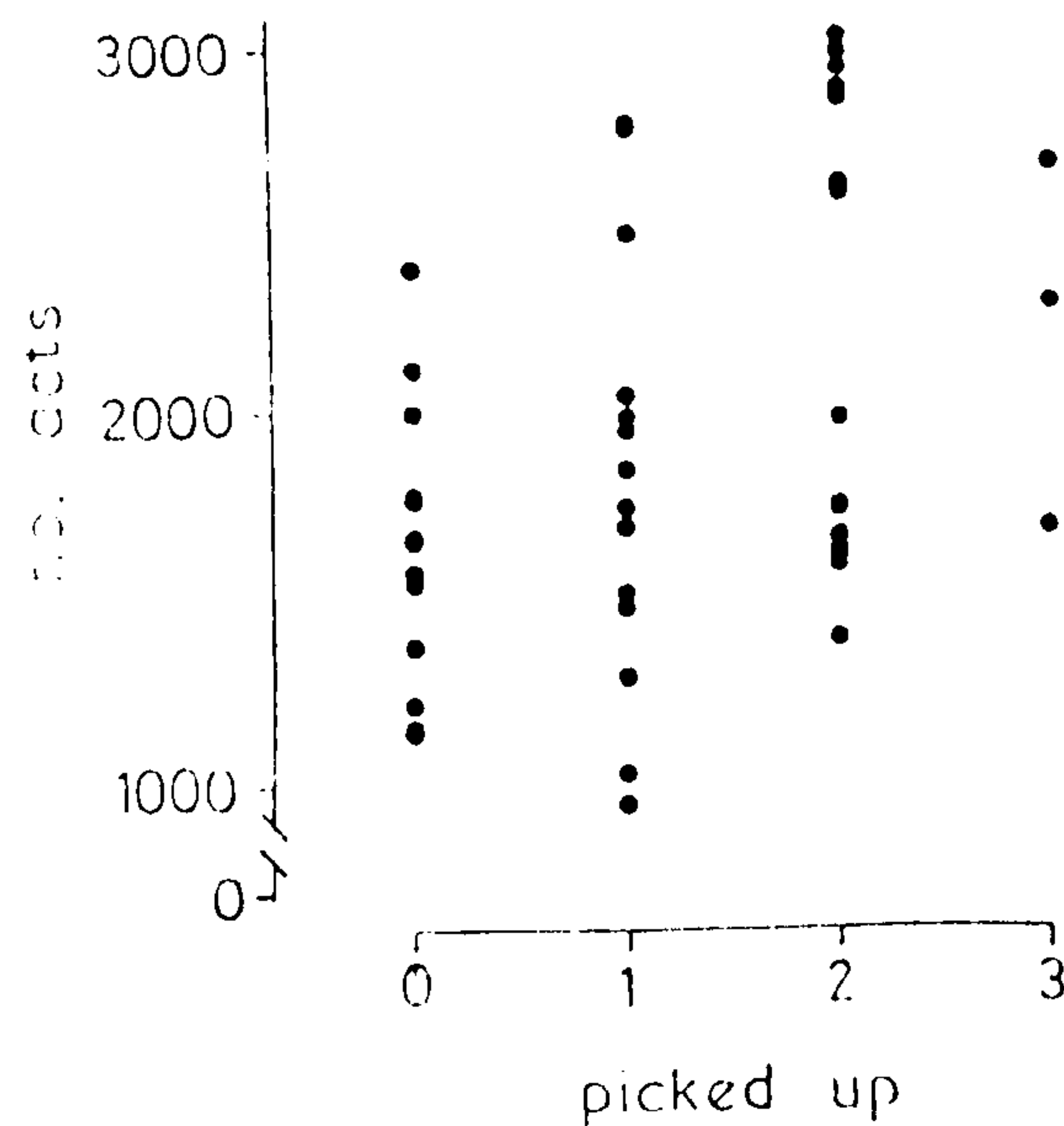


Figure 3.11 The relationship between the composite score (see legend to Figure 3.10) and the number of spermatoophores picked up during amplexus encounters.

Finally, 24 successful captures followed a failed hula display, i.e. involved females which had clearly demonstrated their initial unresponsiveness. Nevertheless, 17 (71 per cent) of these females became inseminated after amplexus.

Hula courtships and Amplexus courtships compared

Of 59 hula courtships involving spermatophore deposition, 18 (30.5 per cent) resulted in insemination, whereas 72 (62.6 per cent) of 115 amplexus courtships were similarly successful. Encounter success was significantly greater for amplexus ($\chi^2 = 16.07$, $P < 0.001$).

Considering the probability of pick up for any spermatophore deposited, 40 (27.9 per cent) of 143 hula spermatophores were picked up, compared with 165 (59.3 per cent) out of 278 amplexus spermatophores. Once again, amplexus is the more successful mode of courtship ($\chi^2 = 37.4$, $P < 0.001$).

The mean number of depositions after amplexus (\pm SEM), 2.34 ± 0.08 , was only 1.7 per cent higher than the number deposited after hula display, 2.3 ± 0.12 ; this difference is not significant ($t = 0.27$, $P > 0.50$).

Aberrant Sexual Behaviour

Aberrant sexual behaviour consists of complete or partial courtship directed towards a member of the same sex. It is most often seen in male-only storage aquaria and consists of both 'homosexual' hula display and amplexus. In the latter, the clasped male will sometimes bend his head downwards, an action which seems similar to the female's rejection posture described by Arnold (1972). In one instance of homosexual amplexus, the clasped male actually elicited the deposition of a spermatophore from the clasper.

Females seldom show such aberrant behaviour, although 'homosexual' amplexus and hula display is sometimes seen in female-only aquaria. A highly responsive female will sometimes respond to a hula displaying male by laterally undulating herself.

Aberrant sexual behaviour of this homosexual type may be the result of 'frustration' (Morris 1955) or 'thwarting' (Hinde 1970) due to an individual being unable to behave sexually in an appropriate social context. In the case of the newt, animals kept in single-sex aquaria, with few opportunities for heterosexual contact, may become frustrated, as Halliday (1974) has suggested for smooth newts. It is interesting to note that in male-male amplexus, the clasped male is often larger than the clasper; perhaps a frustrated, thwarted male sometimes mistakes a larger male for a gravid female. It must be stressed that no individual has been observed to consistently respond in an aberrant manner. Rather, the appearance of aberrant sexual behaviour seems to depend on the immediate social environment of the individual concerned.

3.4.2 An Experimental Analysis of the Male's 'Courtship Decision'

The observations of Arnold (1972) and those described in Chapter 3.4.1 suggest that in dyadic encounters, the male bases his 'decision' of whether to attempt amplexus or perform hula display on the response of the female to his approach. If she moves away from him, he attempts to capture her, but if she stays close by, he performs hula display. The experiment described here was conducted in order to test the validity of this assumption.

Method

A female was taken and anaesthetized in an aqueous solution of MS 222. She was then placed in a strait jacket (see Chapter 2.5).

A male was placed in an observation tank and allowed 10 minutes to settle. The female was then made to approach the male slowly and either remain close to him or move past him. His response to the female was scored as either attempted amplexus or hula display. If he failed to respond in either of these two ways or fled from the female, he was removed. Twenty seven males were tested in all; 12 were given a 'staying female' in the morning and a 'moving female' in the afternoon. The other 15 were subjected to the reverse regime.

Results

The results of this experiment are shown in Table 3.5. As can be seen, amplexus and hula display were significantly related to a 'moving female' and a 'staying female', respectively ($\chi^2 = 11.98$, $P < 0.01$).

| | Male response: | |
|----------------|----------------|----------|
| | Hula display | Amplexus |
| Moving female | 6 | 19 |
| Staying female | 17 | 6 |

$$\chi^2 = 11.98, P < 0.01$$

Table 3.5 The sexual responses of males to females held in strait jackets.

Discussion

This result provides empirical support for the observation that the male's courtship 'decision' is at least partly dependent on the responsiveness of his partner in dyadic encounters. The influence of the ambient sex ratio on the male's courtship 'decision' is considered in Chapter 4.1.

3.5 Activity, Sex and Breathing in the Red-Spotted Newt

Amplexus is a more prolonged type of sexual behaviour than hula display and, given the large disparity in encounter duration which exists (Chapter 3.4.1), it seems likely that the energetic cost of each type of courtship will be different. On the basis of encounter duration, this cost presumably will be greatest for amplexus encounters.

Because male red-spotted newts do not interrupt their courtship in order to breathe, in contrast to the male smooth newt (Halliday and Sweatman 1976), the latency to surface for air at the end of an encounter may provide a crude behavioural index of relative oxygen requirements and thus putative energetic cost. In common with other salamandrid urodeles (e.g. Eddy and McDonald 1978; Halliday and Worsnop 1977), the red-spotted newt obtains oxygen by gaseous exchange across its skin and buccal cavity as well as from its lungs; however, for the present, these accessory routes of uptake will be ignored.

Two experiments are reported in this section. The first considers the relationship between non-sexual locomotor behaviour and breathing, the second that between courtship and breathing. Only males are considered in both experiments.

3.5.1 Non-Sexual Locomotor Behaviour and Breathing

Method

The floor and walls of an observation tank measuring 60 x 30 x 30 cm were marked with parallel lines 10 cm apart. A male was placed in the centre of the tank and, after a settling period of 10 minutes, the whole area of the tank was videotaped for 30 minutes. The videotape record was

then replayed, and the number of lines crossed and number of breathing ascents made by the male were noted. In all, 17 different males were tested in this manner.

Results

As can be seen in the scattergram presented in Figure 3.12, there was a strong positive correlation between the number of lines crossed (activity) and the number of breathing ascents made ($r_s = 0.92$, $P < 0.001$).

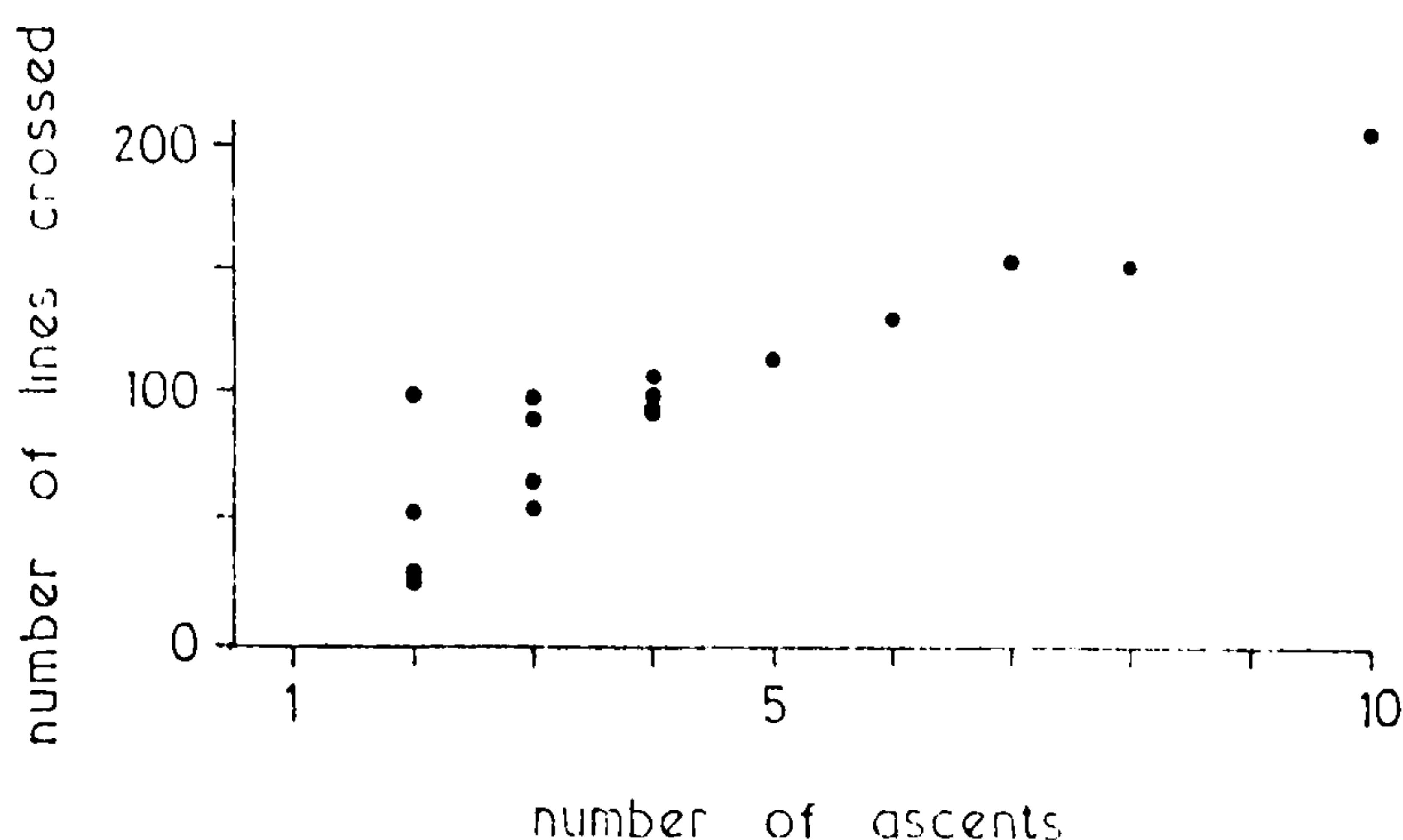


Figure 3.12 The relationship between non-sexual locomotor behaviour (number of lines crossed) and breathing rate (number of ascents) in male red-spotted newts.

3.5.2 Courtship and Breathing

Method

A male and female were placed in an observation tank and the resulting sexual encounter observed in its entirety. Two measures were recorded:

1. the duration of the encounter, defined as the interval from its initiation to the female moving away from the male.

2. the latency to the male's first breathing ascent, defined as the interval from the female moving away to the male's snout breaking the surface of the water.

A total of 13 hula and 13 amplexus encounters were observed, all involving different individuals.

Results

The scattergram in Figure 3.13 shows the relationship between encounter duration and latency to breathe for each type of courtship. No obvious

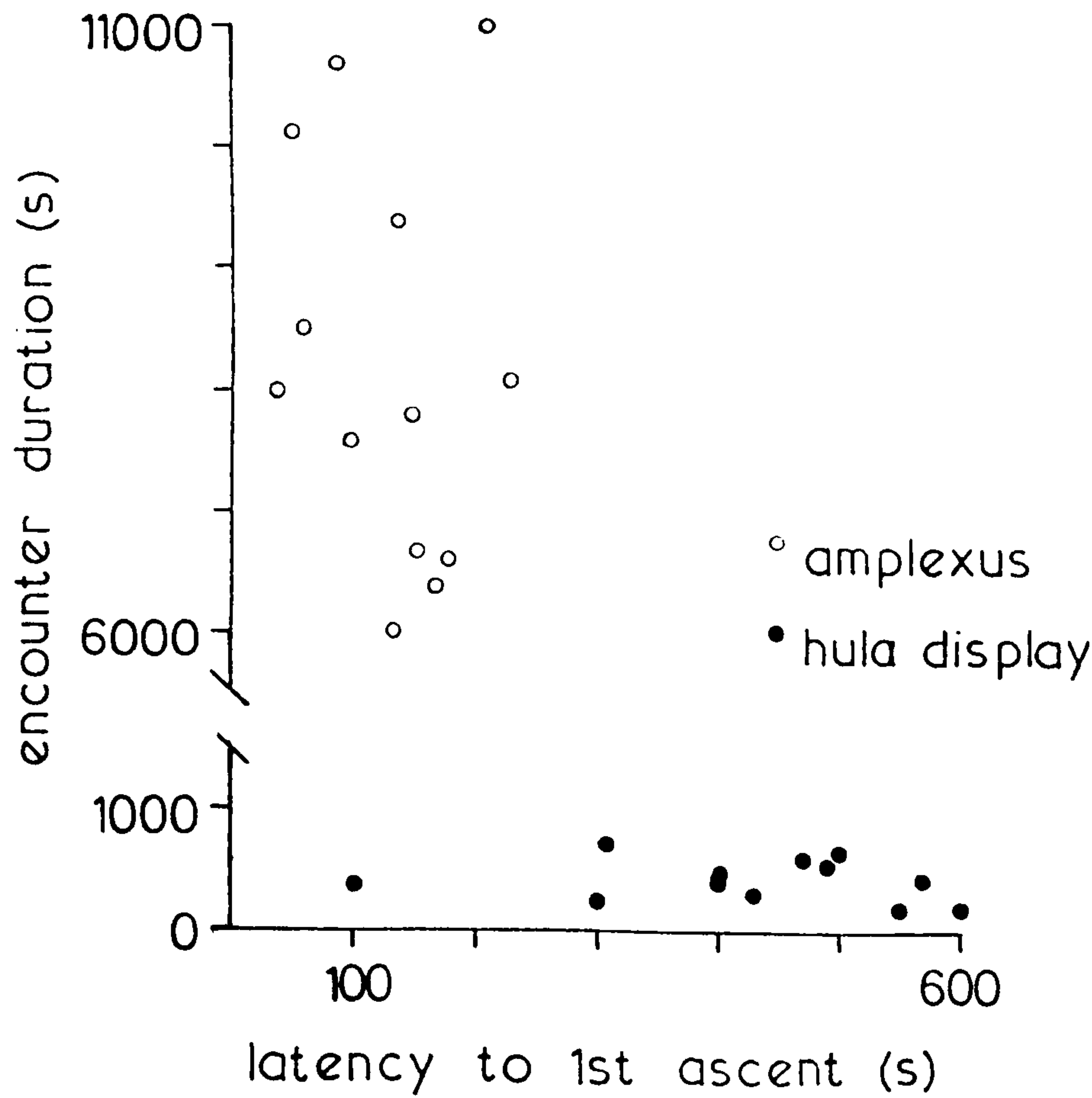


Figure 3.13 The relationship between encounter duration and latency to breathe for male red-spotted newts in each courtship mode. See text for further explanation.

trends are apparent within each type of courtship. However, a comparison between each type reveals that:

1. the mean duration (\pm SEM) of an amplexus encounter, 8253.7 ± 46.6 seconds, is significantly greater than that of a hula encounter, 444.4 ± 50.2 seconds ($t = 16.7$, $P < 0.001$).
2. the mean latency to breathe (\pm SEM) is significantly greater for hula than for amplexus encounters, 434.8 ± 135.3 seconds as against 141.4 ± 17.6 seconds ($t = 7.7$, $P < 0.001$).

3.5.3 Discussion

The results of these experiments support the notion that activity increases the oxygen demand of male newts, and that this demand is greater for amplexus encounters than for hula encounters. Because the water temperature in these experiments remained more or less constant at a mean of 20 C, an influence of temperature on oxygen solubility and/or newt metabolic rate can be discounted.

The relationship between non-sexual activity and breathing rate is not surprising, as oxygen consumption is undoubtedly greater in more active individuals. Halliday and Worsnop (1977) found a similar positive correlation in male smooth newts, using a similar experimental procedure. When their data are recalculated to facilitate a more direct comparison with those presented here, the red-spotted newt is about twice as active as the smooth newts (107 as against 50 lines per 30 minutes), but breathes about half as often (4 as against 7 ascents per 30 minutes). The possible physiological mechanisms and adaptive significance (if any) of these differences are unknown.

That male red-spotted newts breathe more rapidly after amplexus encounters than after hula encounters is also as predicted, and suggests that the energetic cost of the former type of courtship may be greater. Like male smooth newts (Halliday 1977b), male *Notophthalmus* postpone breathing during courtship, but do so far much longer (for up to 3 hours in some amplexus encounters). Whether amplexant males are able to extract sufficient oxygen from their surroundings to maintain aerobic respiration is not known (see Eddy and McDonald 1978). Anaerobic respiration in the lower vertebrates tends to be most common in those species which actively defend themselves against predators, where a sudden burst of activity may be required; aerobic respiration is more common in cryptic and toxic species, i.e. those with 'passive' mechanisms of defense (Bennett 1978, 1980). The red-spotted newt is both cryptic and toxic, but data on the nature of its metabolism are not available.

Thus, despite a lack of detailed biochemical information, it seems that amplexus results in a 'need' for oxygen and, perhaps, incurs an energetic cost considerably greater than that endured by males which perform hula display. Future work on the problem of courtship energetics should concentrate on actual oxygen consumption (e.g. Bucher, Ryan and Bartholomew 1982) and the production of respiratory metabolites (e.g. Putnam 1979).

3.6 Discussion

In this Chapter, I have provided a detailed qualitative and quantitative analysis of the sexual behaviour of single pairs of red-spotted newts. In this discussion, the major results of this analysis are summarized, and the courtship behaviour of *Notophthalmus* compared with that of other animals.

The primary function of sexual behaviour is the transfer of sperm and the subsequent fertilization of ova (Tinbergen 1953). A male red-spotted newt can achieve sperm transfer in one of two different ways, depending on the initial responsiveness of his partner. He assesses the female's state at least partly on the basis of her response to his approach. Hula display occurs if the female is initially responsive and stays close to the male, and it probably provides her with mainly visual stimuli. Hula display encounters are brief (less than 10 minutes in duration) and the probability that the female will become inseminated with at least one spermatophore is low, 30.5 per cent.

Amplexus occurs when the female moves away from the male, signalling initial unresponsiveness, and can be of long duration (up to 201 minutes). Sequences of amplexus do not show the Markov property of stationarity (Cane 1978); that is to say, the probability of one male action following another changes over time. For instance, cheek and forelimb rubbing tend to occur most frequently when bouts of tail vibration are few. The latter occur more frequently when rubbing levels are low. The male's actions provide the female with a range of tactile (cheek and forelimb rubbing, tail vibration and thrashing) and olfactory (cheek rubbing and tail vibration) stimuli. In effect, the male's behaviour during amplexus alters the responsiveness of his partner; evidence for this 'persuasive' or 'aphrodisiac' effect (Arnold and Houck 1982) is derived from two observations

1. that females which reject a hula display may nevertheless become responsive if subsequently amplexed (see Chapter 3.4.1).
2. a composite score, which reflects the total amount of stimulation received by the female, is positively correlated with the number of spermatophores deposited and picked up after amplexus. The male will only deposit spermatophores if the female remains with him (see Chapter 3.4.1).

Such a persuasive function of male display behaviour has been assumed for a long time (see Chapter 5.1), but the literature contains no convincing quantitative data demonstrating a correlation between male display and female willingness to mate (see Robertson 1982; Halliday 1983).

The probability of insemination is 63.6 per cent for amplexus encounters, twice the value for hula encounters. However, amplexus appears to incur a greater energetic cost, as males breathe more quickly after amplexus than after hula display (section 3.5). Within amplexus encounters, there seems to be a trade-off between the 'vigour' of a male's display and the length of time for which he displays; the relevant data are presented in Table 3.2. In general, the amplexant male seems unable to maintain vigorous activity for long periods, again implying some energetic constraint. As discussed in Chapter 3.4.1, the male's display actions are punctuated by periods of relative immobility of varying durations; these may, in some way, ease the energetic burden of the amplexant male.

Thus, in encounters between single males and females, different costs and benefits are associated with each type of sexual behaviour. These are summarized in Table 3.6. Amplexus encounters tend to be lengthy, resulting in a (putative) energetic cost and reducing the rate at which the male can mate with other females. Clearly, a male in amplexus for up to three hours has fewer opportunities to court females per unit time than a male who hula displays for about 10 minutes. However, the amplexant male enjoys a high probability of inseminating his partner. This probability is halved for the male engaged in a hula encounter, but he probably enjoys a lower energetic cost and more opportunities to mate with other females. Although female responsiveness may be the major factor influencing the male's 'decision' of whether to attempt amplexus or hula display, other factors such as the relative abundance of fertilizable females in the population and the male's own 'internal resources' (e.g. sperm availability and

| | Amplexus | Hula display |
|--------------------------------------|----------|--------------|
| effort required to stimulate female | Much | Little |
| rate of encounter with females | Low | High |
| putative energetic cost of courtship | High | Low |
| probability of inseminating female | High | Low |

Table 3.6 Some of the costs and benefits associated with amplexus and hula display as alternative modes of courtship in encounters between single male and female red-spotted newts.

pulmonary oxygen supply) may also play a role. The effects of ambient sex ratio are considered in Chapter 4.1.

This bimodal type of sexual behaviour appears to be unique in the order Urodela. The genus *Notophthalmus* is a member of the family Salamandridae, and its closest extant relatives include the genera *Taricha* (North America), *Cynops* (Japan) and the European *Triturus* (Wake and Ozeti 1969). In *Taricha* and *Cynops*, some form of amplexus is seen during courtship (Smith 1941; Tsutsui 1931). Courtship in *Triturus* consists of a lateral display involving complex tail movements; amplexus is absent (see Chapter 2.2). Halliday (1977a) has suggested that there is a phylogenetic trend in the salamandrids towards reduced male-female contact during courtship. In this respect, the red-spotted newt seems to occupy an intermediate position, for its sexual behaviour includes both amplexus and a modified lateral display (hula display). Nevertheless, the spermatophore transfer stage of courtship in the red-spotted newt very closely resembles that of related newts, suggesting that the principal adaptive radiation in the salamandrid's sexual behaviour has been towards different methods of making the female fully responsive (Halliday 1977a). All of these different methods are composed of some combinations of male actions which provide the female with olfactory, visual and tactile stimulation.

The probability of spermatophore pick up after amplexus in the red-spotted newt is at the upper end of the range of values for salamandrids, whereas the probability after hula display is at the lower end of this range. These data are summarized in Table 3.7. Unfortunately, few data are available for other urodele families. Arnold (1976) has calculated the probability that a spermatophore will be found by the female as 39 per cent for *Ambystoma maculatum* and 61 per cent for *A. tigrinum* (family Ambystomatidae). The probabilities of pick up are not given, but are

| Species | Percentage of spermatophores picked up | References |
|---|--|------------------------------------|
| <i>Notophthalmus viridescens (hula)</i> | 30 | section 3.4.1, this thesis |
| <i>Triturus alpestris</i> | 31 | Halliday (1977a) |
| <i>Ambystoma maculatum</i> | < 39 | Arnold (1976) |
| <i>Triturus vulgaris</i> | 43 | Halliday (1977a) |
| <i>Plethodon jordani</i> | 54 | Arnold (1976) |
| <i>Triturus helveticus</i> | 60 | Halliday (1977a) |
| <i>Notophthalmus viridescens (amplexus)</i> | 60 | section 3.4.1, this thesis |
| <i>Ambystoma tigrinum</i> | < 61 | Arnold (1976) |
| <i>Desmognathus ochrophaeus</i> | c. 80 | L.D. Houck (unpub- lished data) |

Table 3.7 Species differences in the probability of picking up a spermatophore, ranked in ascending order of success.

probably somewhat lower than the figures quoted above. In the family Plethodontidae, pick-up probabilities are 54 per cent for *Plethodon jordani* (Arnold 1976) and about 80 per cent for *Desmognathus ochrophaeus* (L.D. Houck, unpublished data).

The results of Arnold's comparative study suggest that the probability of pick up increases as more courtship is invested in each spermatophore deposited. This investment is measured in terms of courtship duration; this may not be the best measure of investment, but is, of course, easy to quantify. It may result in greater pick up success via an aphrodisiac effect on the female or by coordinating the locomotion of the partners during the spermatophore transfer stage of courtship. Arnold's results are based on interspecific comparisons; in the red-spotted newt, the relationship between investment and pick up success is shown intraspecifically. Pick up success is highest for amplexus encounters, as is the time expenditure per spermatophore deposited. Within amplexus encounters, pick up success is positively correlated with the total amount of stimulation received by the female (see Figure 3.11).

Amplexus, or at least some form of close physical contact, is found in all three major urodele families, the salamandrids, the ambystomatids and the plethodontids, although whether its origins are mono- or polyphyletic is unclear. In all of the species in which close physical contact occurs, the male stimulates the female olfactorily. In many, such as the red-spotted newt, the male applies glandular secretions to the female's nares (Arnold 1977). In others, such as *Desmognathus fuscus*, the male 'inoculates' his secretions into the female's systemic circulation, first abrading her skin with specialized premaxillary teeth (Arnold and Houck 1982).

The bimodal type of sexual behaviour shown by *N. viridescens* represents an example of alternative male mating strategies, discussed further in

Chapters 1.2 and 5.3. For the present, three examples of such strategies with some similarities to the red-spotted newt are given. Female responsiveness determines the nature of the sexual behaviour of male jumping spiders, *Phidippus johnsoni*, and guppies, *Poecilia reticulata*. In the spider, the male can adopt either visual or vibratory courtship, depending on the maturity of his mate and her proximity to her nest (Jackson 1982). The male guppy will court a receptive female, but attempt to forcibly inseminate an unreceptive one; sperm transfer is greatest during courtship (Farr 1980). Male scorpion flies of the genus *Panorpa* usually forage in spider-webs in order to catch insects which are then offered to females in return for copulation; the males of some species offer meals of saliva. Females prefer gift-bearers as mates, and are forcibly inseminated by males without gifts. Sperm transfer is highest during courtship, and the male's 'decision' of whether to court or forcibly inseminate his mate depends on the availability of prey items (Thornhill 1980b).

In none of these examples do males permanently belong to one of a number of distinct classes, e.g. courters or 'rapists'. Rather, as with the male newt, an individual is able to behave flexibly, adopting whichever sexual strategy is appropriate at any given time. In this respect, amplexus and hula display can be regarded as 'conditional' strategies; the male adopts one or other conditional, at least in part, on female responsiveness. In Chapter 4, the effects of ambient sex ratio on the behaviour of male newts are investigated.

CHAPTER 4

SEXUAL SELECTION IN THE RED-SPOTTED NEWT,
NOTOPHTHALMUS VIRIDESCENS

CHAPTER 4

SEXUAL SELECTION IN THE RED-SPOTTED NEWT, *NOTOPHTHALMUS VIRIDESCENS*

In the previous Chapter, the sexual behaviour of the red-spotted newt was examined in isolated pairs. However, in the field, or more correctly, in the pond, pairs probably seldom encounter and court one another in total isolation from conspecifics. In this Chapter, a number of social factors which could influence the sexual behaviour of red-spotted newts are considered.

In Chapter 4.1, the effects of altering the ambient sex ratio in the observation tank are investigated, with the aim of determining if and how this ratio affects the 'decision' of the male whether to attempt amplexus or hula display.

Chapter 4.2 reports experiments involving one female and two males, conducted in order to demonstrate the presence and consequences of competition between males for mates.

In Chapter 4.3, experiments are described which investigate the extent to which females are courted and are inseminated by more than one male.

In Chapter 4.4, evidence is presented to support the contention that, when given a choice, male newts choose to court certain females in preference to others.

Finally, in Chapter 4.5, the sexual behaviour of the red-spotted newt is discussed as a complex set of strategies.

4.1 The Influence of Ambient Sex Ratio on the Sexual Behaviour of the Male Red-Spotted Newt

The bimodal sexual behaviour of the red-spotted newt, described in Chapter 3.4 for dyads, is controlled, at least in part, by the initial responsiveness of the female partner. However, in nature, courtship encounters probably seldom occur in such isolation from conspecifics; other individuals of both sexes are likely to be in the vicinity of a male searching for a mate. When the male encounters a female, he either attempts to capture her or performs hula display to her. These two types of courtship differ greatly in their consequences for the male; the relevant costs and benefits of each were discussed in Chapter 3.6 (summarized in Table 3.6). Encounter success, in terms of spermatophores transferred, is highest for amplexus, as are the putative energetic costs of courtship. The potential for mating with several females per unit time is highest for hula encounters. Given these disparities in costs and benefits, it was predicted that the male should be 'sensitive' to the ambient sex ratio in his vicinity; more specifically, that if females are freely available, he should abandon amplexus in favour of hula display, thus escaping the costs associated with the former mode of courtship. This prediction carries the assumption that the male is able to mate repeatedly over a fairly short period of time. Evidence for such an ability is weak, and rests on a number of anecdotal observations of males finishing one encounter and then initiating another a few minutes later.

The first series of experiments described in this section was designed to test the validity of the prediction stated above. In addition, a second series was conducted in order to investigate the effects of an ambient sex ratio skewed towards an excess of males on the behaviour of a courting male.

4.1.1 Is the Male's Behaviour a Function of Female Density?

Method

All experiments consisted of 40 trials, all using unique combinations of individual newts (40 males and 30 females). In the first experiment, a male and female were placed in an observation tank and the first sexual action of the male (either amplexus or hula display) and the preceding action of the female (either move away or stay still) were recorded. In the second experiment, a male was placed with eight females. Only the male's actions to the first female actively encountered and her preceding behaviour were recorded, as for the first experiment in this series.

Results

Figure 4.1 shows the responses of males to females in each of the two experiments. As discussed in Chapter 3.4, the male should attempt amplexus if the female moves away from him. The results presented here support this, and no difference was detected between the one-female and eight-females conditions.

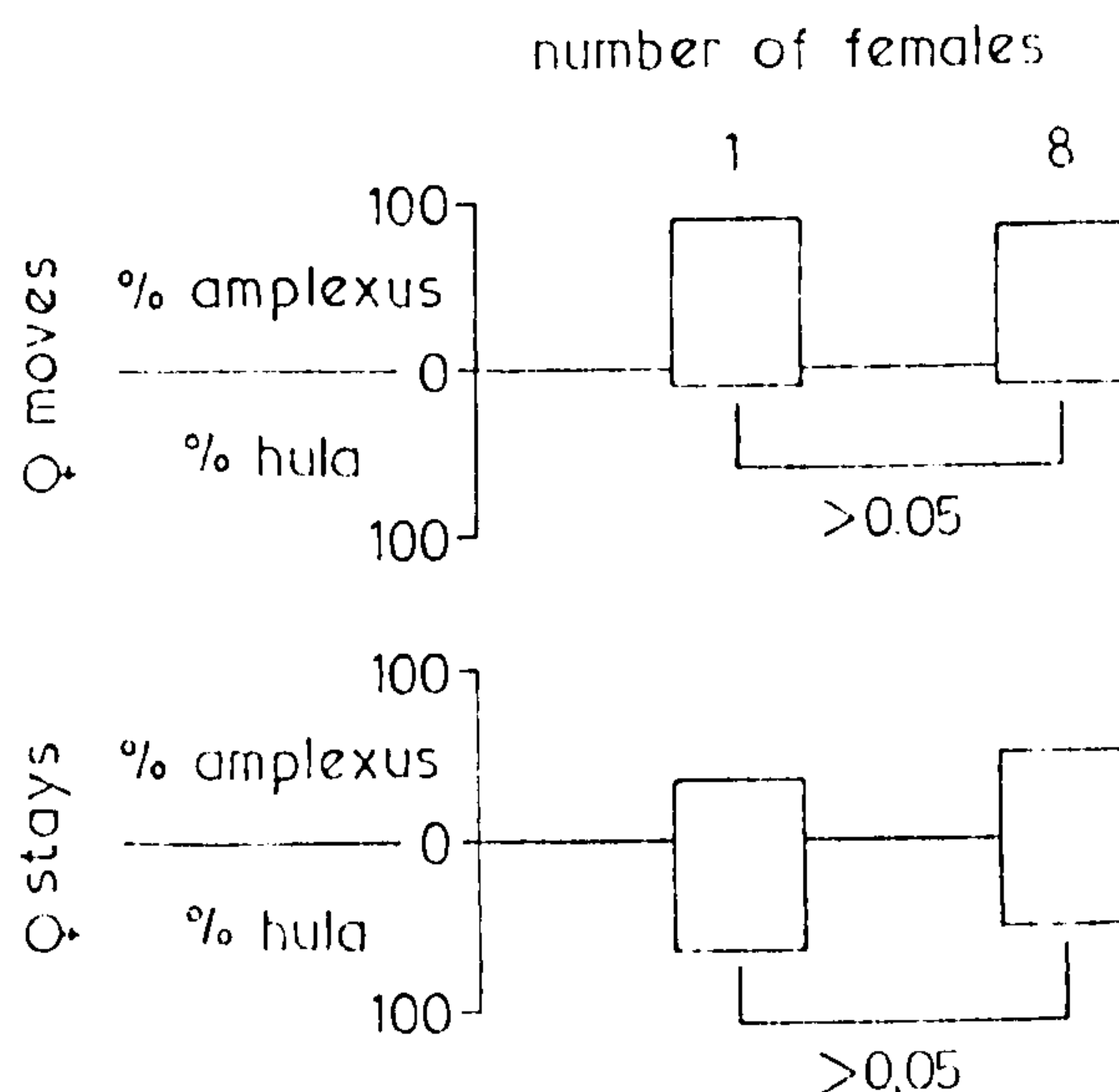


Figure 4.1 The responses of male red-spotted newts (either amplexus or hula display) as a function of female density.

When the female stays close to the male, he should perform hula display. Once again, the data in Figure 4.1 support this. However, the males' responses were not affected by female density and thus the prediction formulated above, of a shift to hula display at high female densities, is not supported.

4.1.2 Is the Male's Behaviour a Function of Male Density?

Method

All experiments consisted of 40 trials, using unique combinations of newts in each (50 males and 30 females). In the first experiment of this series, a male and female were placed together and their behaviour recorded as described in Chapter 4.1.1. In the three subsequent experiments in this series, one, three and seven extra males were placed in the observation tank, and the behaviour of the first male to respond sexually to the female, and her preceding behaviour, were recorded.

Results

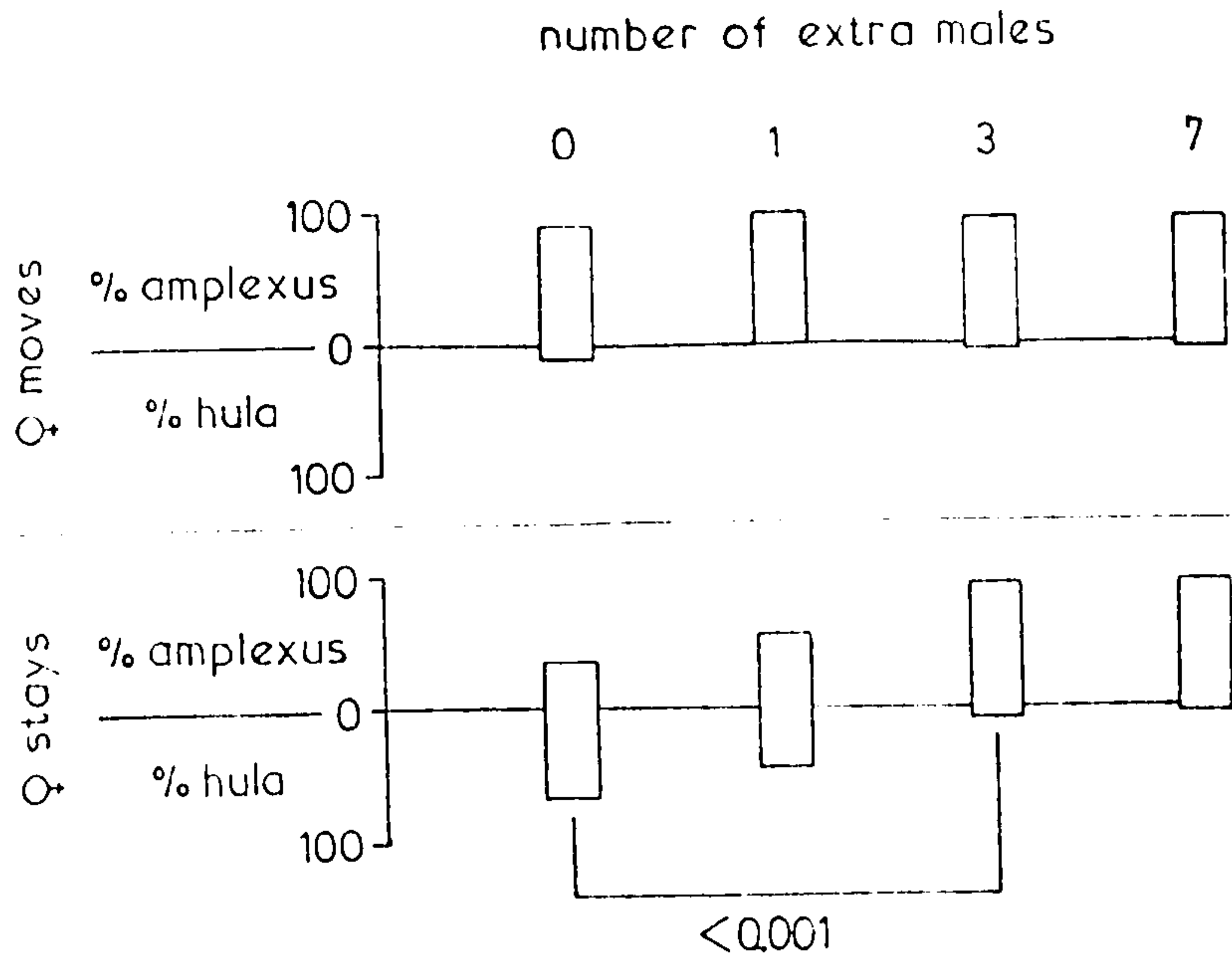


Figure 4.2 The responses of male red-spotted newts (either amplexus or hula display) as a function of male density.

The relevant data are summarized in Figure 4.2. When the female moved away, the males attempted amplexus regardless of the number of other males in the vicinity. However, when the female remained close to the males, the presence of other individuals resulted in a greater tendency to adopt amplexus.

4.1.3 Discussion

The results of these experiments demonstrate that in a complex social environment, the decision of a male whether to attempt amplexus or hula display is not affected by the density of females available, but is influenced by the density of males in the vicinity, the opposite to the predicted effect. In the presence of other males, a courting male shows a tendency to adopt amplexus, regardless of the female's responsiveness; in dyadic encounters, female responsiveness plays an important part in determining which type of courtship the male attempts. The possible function of this shift to amplexus in the presence of other males is considered next.

4.2 Sexual Interference and Defense in the Red-Spotted Newt

The experiments described in Chapters 2.4 and 2.5 provide evidence for sexual interference and sexual defense in the smooth newt. Only one anecdotal report of interactions between males is available in the literature on the red-spotted newt; Pope (1924) describes how a single female may be the focus of attention of several males. D.E. Gill (personal communication) has observed unpaired males apparently attempting to displace males in amplexus.

In this section, I report experiments designed to investigate the nature and extent of reproductive competition in red-spotted newts, and suggest that such competition may account for the shift to amplexus described in Chapter 4.1.2.

4.2.1 Competitive Amplexus Encounters

Method

Two males and a female were placed in an observation tank and all interactions between the animals videotaped for a single amplexus encounter. A total of 55 such encounters were recorded, all involving different combinations of animals from a pool of 50 males and 30 females.

Results

Of the 55 encounters observed, interactions between the males occurred in 38 (69 per cent). The 17 encounters which were free from such interactions proceeded in a manner more or less identical to that described in Chapter 3.4.1 for encounters between single males and females.

In 33 (60 per cent) encounters, the unpaired male, or rival, interacted with the paired male, or courter, whilst the latter was clasping the female. The rival would slowly approach the courting pair and suddenly 'vault' onto the dorsum of the courter. In this position, with his hindlimbs gripped around the courter's body, the rival male would attempt to 'burrow' between the courter and the female, pushing with his snout and forelimbs. In four encounters involving this action, the rival male successfully displaced the courter from the dorsum of the female, but in only one did he manage to initiate amplexus with her himself; in the other three cases, the female escaped as the take-over was attempted.

The courter responded to attempted displacement by the rival by ceasing to display to the female with cheek and forelimb rubbing, head and tail turning and tail vibration. In all, 60 attempted displacements were observed. In 33 (55 per cent), the courter remained totally motionless, the rival detaching himself after a few minutes. In 23 (38 per cent), the courter thrashed about on the substrate, leading to the rival being shaken free from the amplexant pair. In a few encounters, the courter crawled away from the rival when the latter was detached, pulling himself and the female across the substrate with his forelimbs. When the rival was detached, the courter would resume displaying to the female.

The mean number of such displacement attempts made by the rival per encounter (\pm SEM) was 1.26 ± 0.17 , with a range of 0-4. As Figure 4.3 shows, the mean duration of amplexus was significantly higher in those encounters in which the rival attempted at least one displacement. The scattergram in Figure 4.4 reveals a positive correlation between the eventual duration of amplexus and the number of displacement attempts made by the rival ($r_s = 0.69$, $P < 0.001$). That this correlation is not merely a consequence of longer encounters offering more opportunities for displacement is suggested by the fact that mean duration of amplexus is higher in encounters involving displacement attempts than it is in attempt-free encounters.

At the end of amplexus, the courter dismounts from the female and initiates the spermatophore transfer stage of courtship. In 13 (23.6 per cent) of the 55 encounters observed, the rival interfered during this stage; in 11 of these 13 instances, the rival had previously attempted (unsuccessfully) to displace the amplexant courter. Sexual interference during the spermatophore transfer stage of courtship was of the female mimicry type, and resembled that described in Chapter 2.4.1 for the smooth newt. Figure 4.5 shows such sexual interference in *Notophthalmus*. As

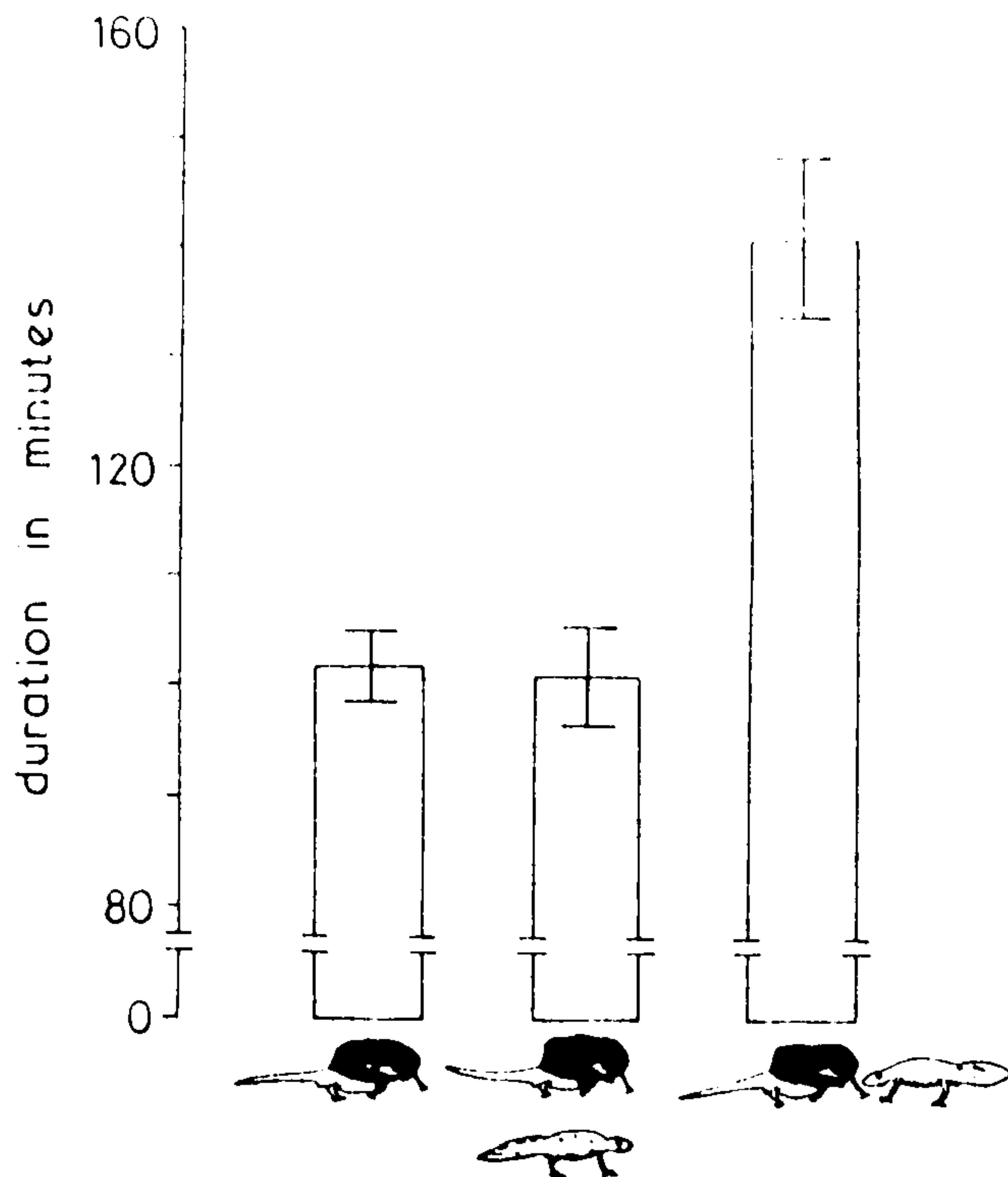


Figure 4.3 The duration of amplexus. Left: dyadic encounters; centre: triadic encounters in which no attempts at displacement were made; right: triadic encounters in which at least one attempt at displacement was made.

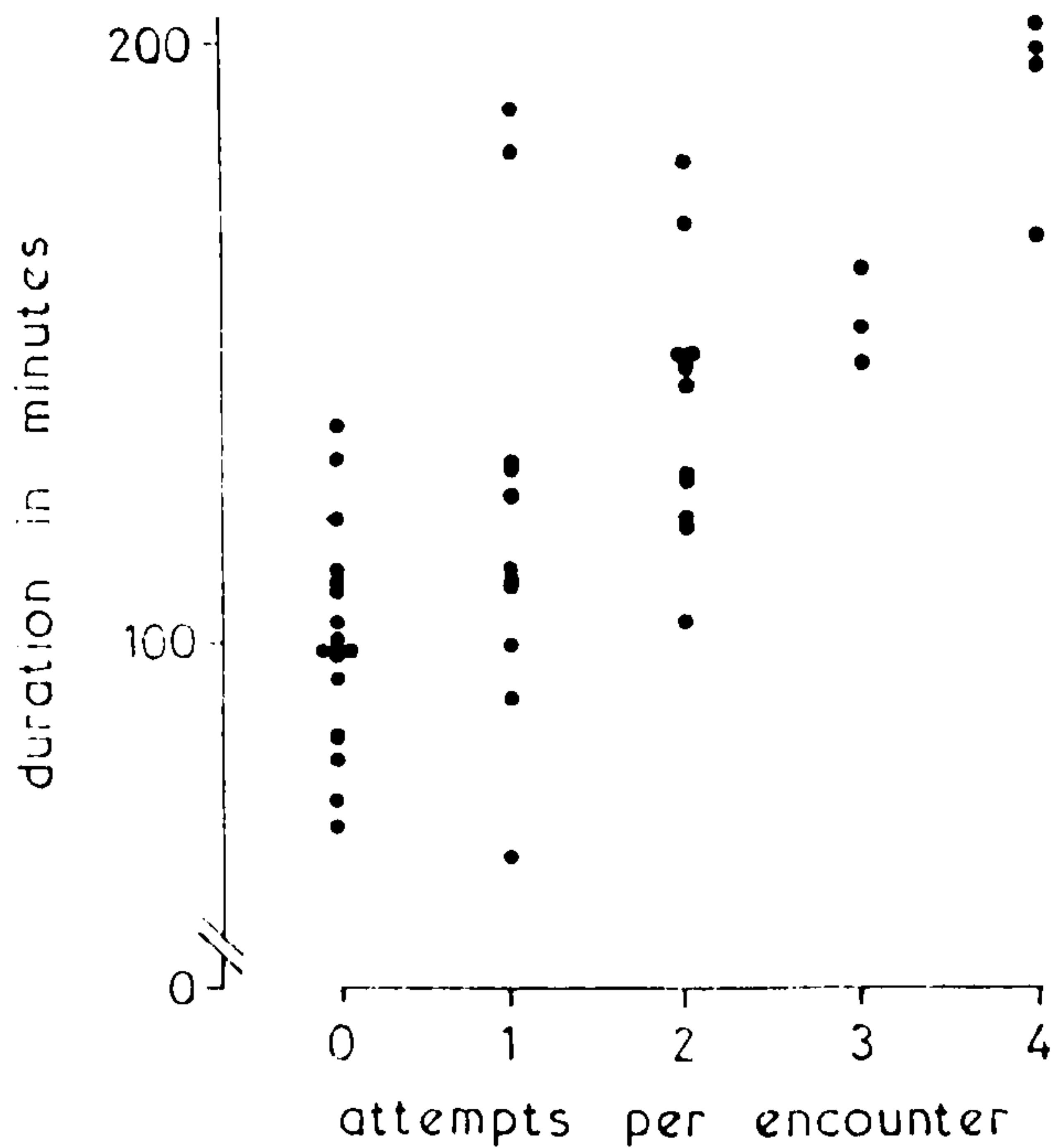


Figure 4.4 The relationship between the duration of amplexus and number of attempts at displacement made during triadic encounters.

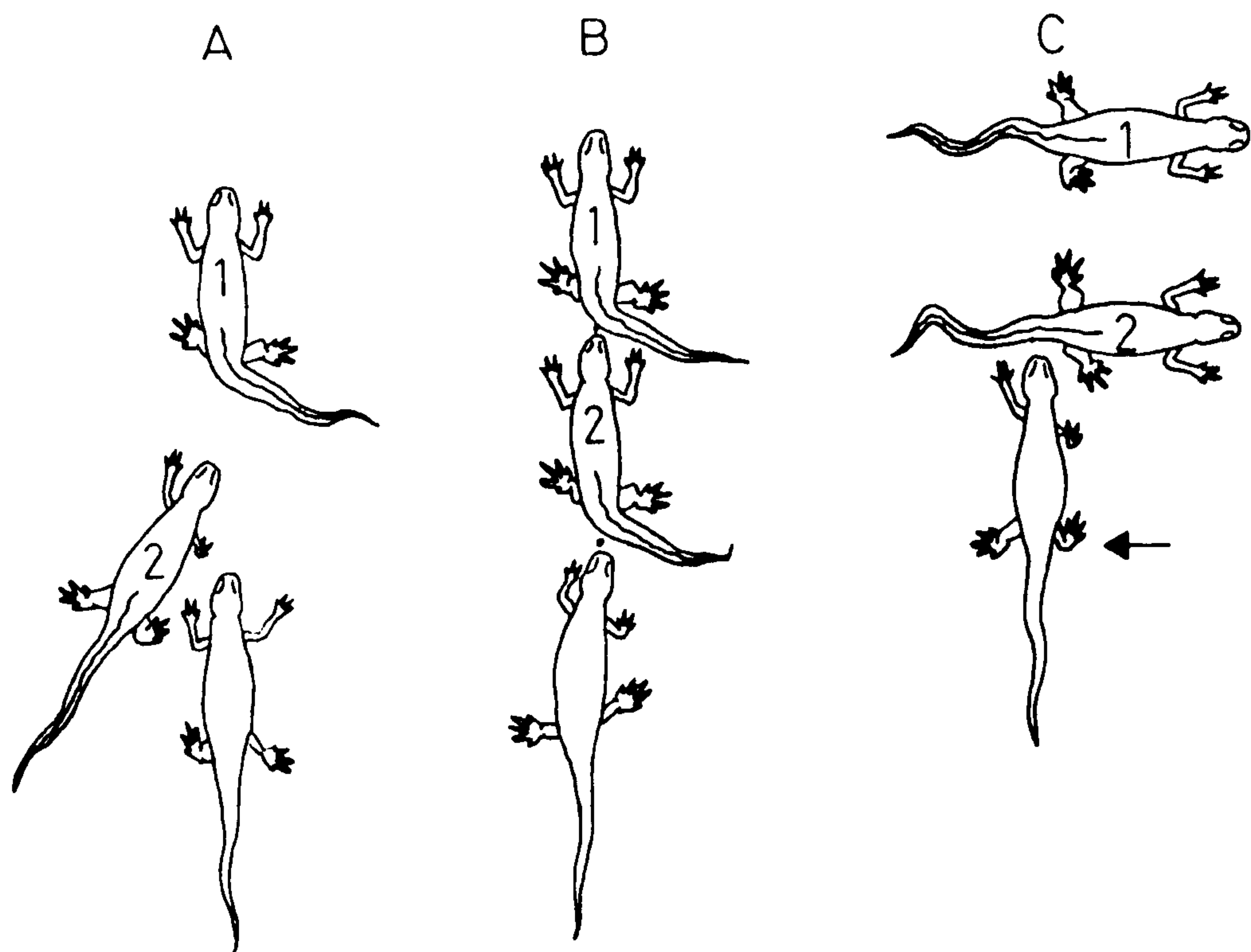


Figure 4.5 Sexual interference by female mimicry in the red-spotted newt. A: as male 1 creeps in front of the female, male 2 moves between the pair; B: male 2 then elicits the deposition of a spermatophore from male 1. The female nudges male 2's tail and causes him to deposit also; C: both males creep-on, but only male 2's spermatophore is available to the female (arrow).

| | Female: | |
|------------------------|-------------|-----------------|
| | inseminated | not inseminated |
| With female mimicry | 27 | 11 |
| Without female mimicry | 9 | 4 |

$x^2 = 0.017, P > 0.10$

Table 4.1 The probability of the courter transferring at least one spermatophore to the female in amplexus encounters with and without female mimicry.

the courter crept away from the female, 'inviting' her to follow, the rival placed himself between the partners. By nudging at the courter's tail with his snout, the rival was able to elicit the deposition of a spermatophore from the courter. The latter would then enter the highly stereotyped creep-on movement which follows deposition, leaving the female with the rival. In four (31 per cent) of the 13 instances of this behaviour, the female remained with the rival, nudged his tail and elicited spermatophore deposition. In three instances, the females involved picked up the rivals' spermatophores; in one, the one the female had already picked up sperm from the courter.

Table 4.1 compares the probability of the courter transferring at least one spermatophore to the female in the absence and the presence of a rival that mimicks female behaviour. Sexual interference of this sort did not significantly alter the success of the courter ($\chi^2 = 0.017$, $P > 0.05$).

4.2.2 Competitive Hula Encounters

Method

When a male encounters a female in the presence of other males, he tends to clasp her whether or not she is responsive towards him (see Chapter 4.1.2).

Because of this shift to amplexus, it proved difficult to collect data on sexual interference during hula encounters. The method used was rather unsatisfactory. Male and female were placed together and, if hula display ensued, another male, the rival, was carefully introduced about 30 seconds after the courter had initiated his display. The data presented here are derived from 46 hula encounters, involving different combinations of individuals from a pool of 46 males and 30 females.

Results

Of the 46 encounters observed, competitive interactions between the two males occurred in 32 (70 per cent). These interactions were all similar in form to sexual interference by female mimicry as described in Chapter 4.2.1. The rival male deposited a spermatophore in response to tail nudges from the female in 22 (69 per cent) of these encounters, and the female was inseminated by the rival in 13 (41 per cent). In two of these, the female had already picked up sperm from the courter.

Table 4.2 compares the probability of the courter transferring at least one spermatophore to the female in the absence and the presence of a rival mimicking female behaviour. Sexual interferences significantly altered this measure of success ($\chi^2 = 3.77, P < 0.05$).

| | Female: | |
|------------------------|-------------|-----------------|
| | inseminated | not inseminated |
| Without female mimicry | 7 | 7 |
| With female mimicry | 24 | 8 |

$$\chi^2 = 3.77, P < 0.05$$

Table 4.2 The probability of the courter transferring at least one spermatophore to the female in hula encounters with and without female mimicry.

4.2.3 Discussion

The results presented here demonstrate that sexual interference occurs in the red-spotted newt. During an amplexus encounter, the courting male is assaulted by rivals which attempt to displace him from the female; however, such attempts seldom seem to be successful. The amplexant

male responds to such attempts by either remaining motionless, in which case the rival detaches himself, or by thrashing about, apparently in order to shake off the rival. The amplexant male also responds to attempted displacements by remaining in amplexus for longer than in dyadic encounters (Figure 4.3); the duration of amplexus increases as more attempts are made. When the courter dismounts, he is vulnerable to sexual interference by female mimicry. A rival is most likely to behave as a female mimic if he previously attempted to displace the courter during amplexus. Although sexual interference during the the spermatophore transfer stage of courtship does not significantly affect the probability of the courter inseminating the female, it does enable the rival to usurp the courter so that he can inseminate her himself.

Sexual interference by female mimicry also occurs during hula encounters; however, it must be remembered that hula encounters seldom occur in the presence of other males (see Chapter 4.1.2). Female mimicry lowers the courter's insemination success, and also enables the rival to gain inseminations.

Comparing sexual interference by female mimicry for amplexus and hula encounters, it is more likely to occur during the latter; 32 (69.6 per cent) of 46 hula encounters as against 13 (23.6 per cent) of 55 amplexus encounters ($\chi^2 = 21.5$, $P < 0.001$). However, the rival was no more likely to inseminate the female during hula encounters, 13 (40 per cent) of 32, than during amplexus encounters, 3 (23 per cent) of 13 ($\chi^2 = 2.75$, $P > 0.05$).

I suggest that the major methods of sexual defense in the red-spotted newt consist of 1) a shift to amplexus in the presence of other males (which are potential rivals) and 2) increasing the duration of amplexus if the rival attempts to displace the courter. In these respects, amplexus

in the newt appears to be functionally analogous to other forms of physical mate guarding, especially the precopulatory passive phase adopted by many arthropod species. In this phase, the male mounts the female, although their genitalia remain uncoupled, and he defends her against the advances of other males (Parker 1970; 1974). By shifting to amplexus irrespective of initial female responsiveness, the courter is able to avoid the high incidence of sexual interference which seems to affect hula encounters.

As in the smooth newt (see Chapter 2.4.1), sexual interference significantly alters the insemination success of a male red-spotted newt, but only for hula encounters. It also sometimes leads to the female being multiply inseminated, first by the courter and then by the rival. This may result in sperm competition within the female's genital tract, a possibility discussed in more detail in Chapters 4.3 and 5.2.2.

In a comparative context, attempted displacement during amplexus as a form of sexual interference has only been described for two genera in the family Salamandridae, *Taricha* (Ritter 1897; Smith 1941; Arnold 1977) and *Pleurodeles* (Arnold 1977). Although sexual interference by female mimicry occurs in a number of salamander species (Arnold 1976, 1977), it has only been described for two salamandrid species, the smooth newt and the red-spotted newt. Reproductive competition in the urodeles is further considered in Chapter 5.2.

4.3 Multiple Mating by Female Red-Spotted Newts

Sexual interference sometimes results in a female red-spotted newt being inseminated by more than one male in rapid succession (Chapter 4.2). As suggested for the smooth newt in Chapter 2.6, multiple insemination may result in sperm competition, a further type of intrasexual competition

(Halliday and Verrell 1983). In this section, I describe two experiments designed to investigate the extent of multiple mating by female red-spotted newts.

4.3.1 Experiment One

Method

This experiment was conducted in the spring breeding season of 1981. Nineteen females were allowed to become inseminated with a single spermatophore, and were then placed together in a single storage aquarium.

These females were then assigned at random to one of three groups, of unequal size. Each group was tested by placing the females with males for one hour or one sexual encounter, either one day (N = 8), five days (N = 7) or eight days (N = 4) after their initial insemination. The number of females in each group which picked up at least one spermatophore in a test was recorded.

Results

| Time since last spermatophore picked up | Number of females which: | |
|---|--------------------------|---------------------------|
| | were tested | picked up a spermatophore |
| 1 day | 8 | 4 |
| 5 days | 7 | 2 |
| 8 days | 4 | 1 |

Table 4.3 The responses of three groups of inseminated females to further male courtship.

Table 4.3 summarizes the results of this experiment. Despite the small sample sizes of each group of females, it is clear that some inseminated females remained responsive to further male courtship for up to eight days after their initial insemination.

4.3.2 Experiment Two

Method

This experiment, conducted in the spring of 1981, was conceived in an attempt to raise newt tadpoles in the laboratory (see Verrell, in press). Data relevant to multiple mating were collected incidentally.

Thirteen females were inseminated with variable numbers of spermato- phores and the course of oviposition recorded for each female. Some of these females were remated at variable intervals after their initial insemination.

Results

The relevant data are presented in Table 4.4. Two points of interest emerge in the context of multiple mating. First, females which ceased to lay eggs after a single courtship did not resume laying when they remated (females 1, 5, 9 and 12 in Table 4.4).

Secondly, females which did not lay any eggs after their initial courtship did not necessarily begin laying when they remated (female 4 did, females 2 and 6 did not).

| female | number of eggs laid | was female remated? | did female lay more eggs? |
|--------|------------------------|------------------------|------------------------------|
| 1 | 56 | yes | no |
| 2 | 0 | yes | no |
| 3 | 52 | no | - |
| 4 | 0 | yes | yes, 34 |
| 5 | 101 | yes | no |
| 6 | 0 | yes | no |
| 7 | 21 | no | - |
| 8 | 23 | died | - |
| 9 | 58 | yes | no |
| 10 | 0 | died | - |
| 11 | 48 | no | - |
| 12 | 78 | yes | no |
| 13 | 20 | died | - |

Table 4.4 The breeding efforts and consequences of remating in a group of 13 females.

4.3.3 Discussion

Small sample sizes preclude any detailed analysis of the results presented in this section, but it is clear that inseminated females will remate if exposed to further male courtship. The potential thus exists for sperm competition, as discussed further in Chapter 5.2.2.

The data from the second experiment demonstrate that not all inseminations necessarily result in the production of fertilized eggs. This may be an artefact of the experimental procedure followed, but, if it occurs in the field, it implies that not every mating procured by a male results in him fathering any offspring. The data do, however, provide further evidence for remating by females.

4.4 Mate Choice in Male Red-Spotted Newts

In Chapter 2.7.2, it was demonstrated that male smooth newts prefer to remain in the vicinity of larger rather than smaller females, and that female fecundity is positively correlated with body size. It was suggested that, by exhibiting such a preference, males are able to maximize their reproductive success.

In this section, I describe two experiments designed to test the hypothesis that male red-spotted newts 1) prefer to remain in the vicinity of larger females and 2) prefer to court such females. The functional basis of this prediction is the relationship between female fecundity and size. Some details of the second experiment have already been published (Verrell 1982d).

4.4.1 Vicinity as an Indicator of Mate Choice

Method

Full details of the experimental procedure are given in Chapter 2.7.1. Twenty different males were given the choice between two females differing by at least 0.5 g in weight and 5 mm in length.

Results

The histograms in Figure 4.6 present the results of this experiment. Statistical analysis was conducted as described in section 2.7.1. Males distributed themselves non randomly with respect to the two test females (Table 4.5), showing a tendency to remain in the vicinity of the larger female, as established using the non-parametric sign-test.

4.4.2 Courtship as an Indicator of Mate Choice

Method

A male newt was placed in an observation tank and allowed 10 minutes to settle. Two females differing by at least 0.5 g and 5 mm were then placed with the male. The newts were observed for a period of 20 minutes, during which time the latency to the first sexual action of the male (amplexus or hula display) and the number of such actions directed to each female were recorded. Forty such trials were conducted, all involving different individuals.

In order to verify that female fecundity is correlated with body size in this species, 15 females were sacrificed, and the number of yolked oocytes in the ovaries counted.

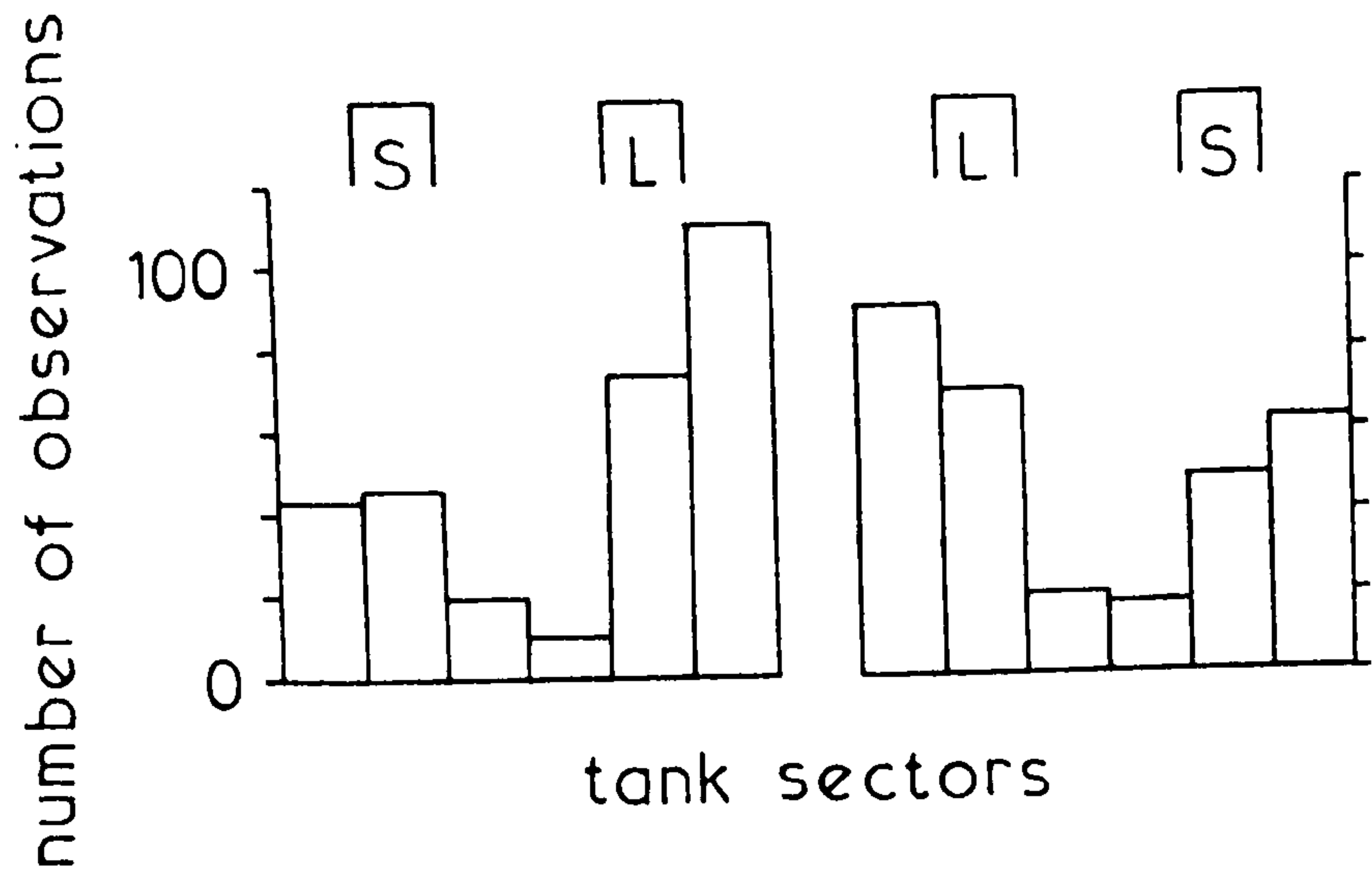


Figure 4.6 Histograms showing the responses of male red-spotted newts to small (S) and large (L) females. Statistical analysis of these data is presented in Table 4.5.

| | |
|----------------------------|----------------------------|
| Small female, large female | Large female, small female |
| P < 0.02 | P < 0.02 |

Table 4.5 Results of sign-tests conducted on the data for individual males summarized as histograms in Figure 4.6.

Results

A total of 117 sexual actions were observed over the 40 trials. Seventy six actions were directed towards the larger female, 41 towards the smaller female; males directed significantly more actions towards the larger female ($\chi^2 = 10.5$, $P < 0.001$). The mean latency to approach the larger female first in a trial, 367.7 ± 47 seconds, was not significantly different from that for approaching the smaller female first, 400.0 ± 77 seconds ($t = 0.36$, $P > 0.05$).

A positive correlation was found between female snout-vent length and the number of yolked oocytes in the ovaries ($r = 0.8$, $P < 0.001$; see Figure 4.7).

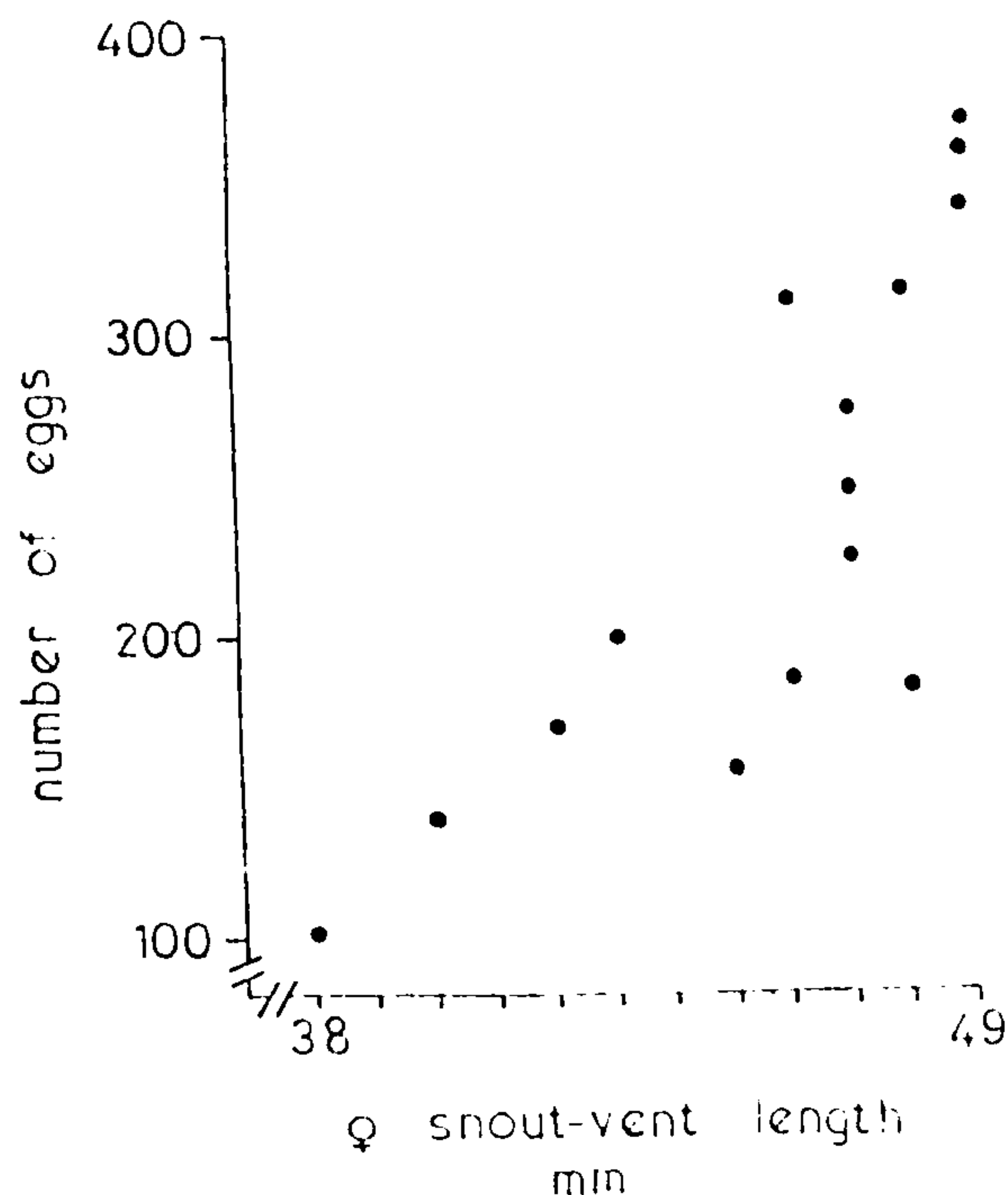


Figure 4.7 The relationship between female length and the number of yolked oocytes in the ovaries.

4.4.3 Discussion

The results presented above support the hypothesis that male red-spotted newts choose larger females as their mates, and that female fecundity is positively correlated with size. That this is an active choice, and

not merely a consequence of larger females being more conspicuous and easier to locate, is suggested by the fact that males do not respond to larger females more rapidly than to smaller ones.

Mate choice in the red-spotted newt appears to maximize a male's reproductive success, because he inseminates females containing large numbers of eggs. In general, the extent to which males are choosy is expected to vary with their parental investment (see Halliday 1983). Males have been shown to mate selectively with larger, more fecund females in a number of species in which males make a substantial investment in reproduction by transferring nutrients, as well as sperm, during copulation, e.g. the Mormon cricket, *Anabrus simplex* (Gwynne 1981), and the checkered white butterfly, *Pieris protodice* (Rutowski 1982).

Male newts are believed to provide their mates with nothing but sperm, although the possibility of nutrient transfer has yet to be empirically investigated. However, the male does not continue to produce mature spermatozoa during the course of the breeding season. Spermatogenesis is completed soon after the end of the breeding season, and the mature gametes are held over in the testis until the following spring (Adams 1940; Lofts 1974). Each mating thus depletes the male's limited sperm supply and, this being the case, mate choice aimed at maximizing reproductive success would be expected. Selective mating with more fecund females would have just this result. Evidence that larger females actually lay more eggs was derived indirectly by analysis of the data presented in Chapter 4.3.2. A positive correlation existed between female length and clutch size for those females which actually laid eggs ($r = 0.7$, $P < 0.05$).

In a wider context, these results suggest that male mate choice may evolve in those situations where sperm supplies are limited. Dewsbury (1982) and Nakatsuru and Kramer (1982) have questioned the widely held belief that

males produce almost unlimited supplies of sperm, and suggest that sperm limitation, which may be a common phenomenon in animals, may favour males exercising choice of mates.

4.4.4 A Comment on Female Mate Choice

An experiment was conducted in order to ascertain whether female red-spotted newts choose their mates on the basis of size. Unfortunately, this experiment was never completed, because the females being used showed a rapid loss of breeding condition accompanied by a tendency to leave the water.

4.5 An Overview of the Sexual Behaviour of the Red-Spotted Newt

The results of the experiments reported in this Chapter suggest that the complex sexual behaviour of the red-spotted newt has evolved, at least partly, under the influence of sexual selection. Males compete amongst one another for the insemination of females and choose larger, more fecund females for their mates. Much of the evidence for sexual selection has been evaluated at the end of each section and some points are discussed further in Chapter 5.

In this section, the complexity of the sexual behaviour of the red-spotted newt is considered. During a single sexual encounter, the male is faced with a number of decisions: is the female already being courted? is she receptive? are other males present? These decisions, and the male's responses to them, are summarized in Figure 4.8. If the female is already being courted, the male attempts to usurp the male she is with and inseminate her himself. If the female is alone, the male assesses her receptivity; if she is not receptive, he initiates amplexus with her.

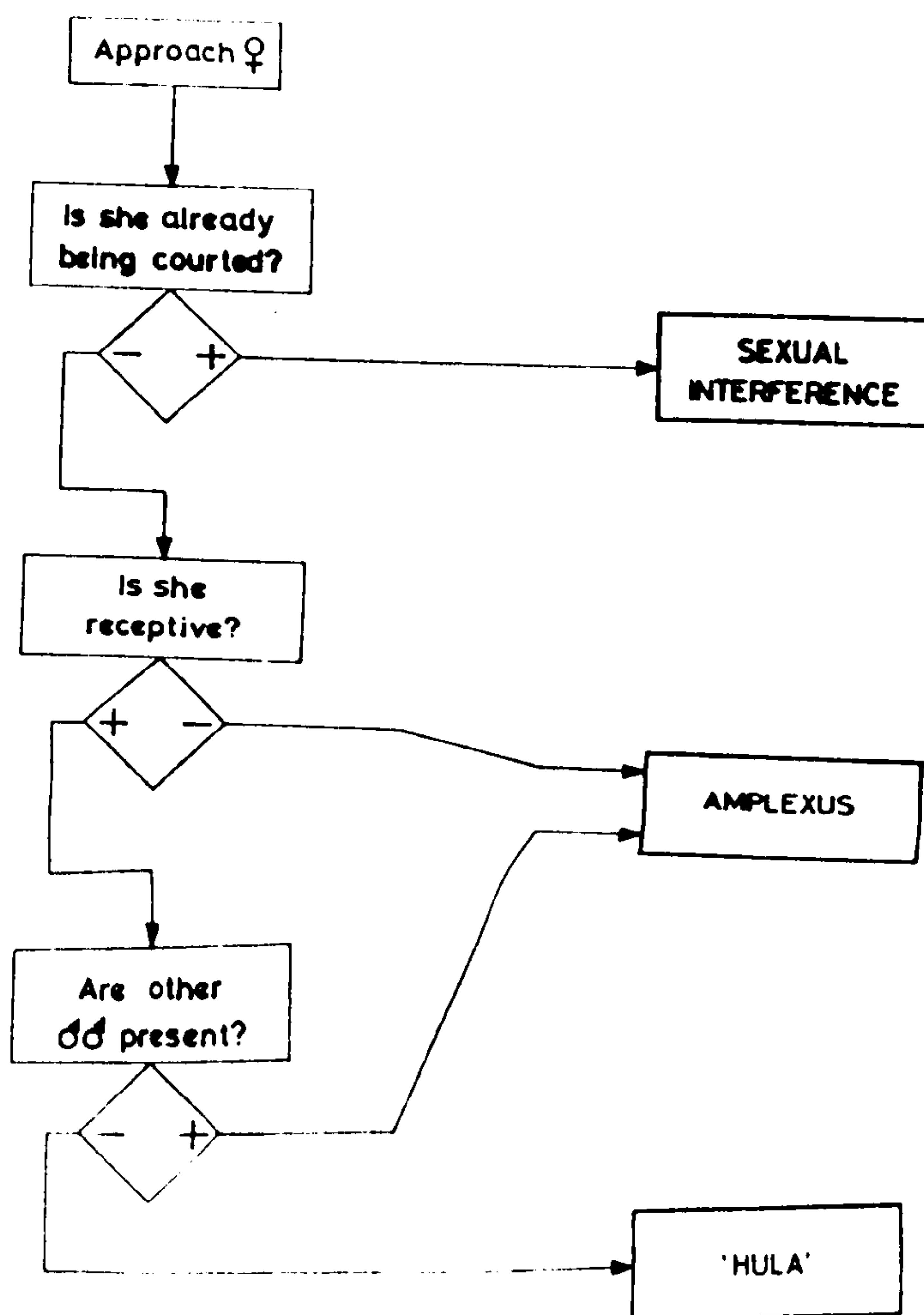


Figure 4.8 The 'decisions' faced by a male red-spotted newt during a sexual encounter. - is the answer 'no', + is the answer 'yes'.

If she is receptive, he performs hula display. However, the male only performs hula display if there are no other males in the vicinity. If other males are present, he initiates amplexus.

The various responses available at each decision-point in an encounter differ greatly in their consequences. The costs and benefits associated with each response are shown in Table 4.6, each response being considered as an alternative mating strategy. As discussed in Chapter 4.1, the male is unlikely to encounter females in the total absence of other males and thus the strategy 'hula' may be seldom observed in natural breeding populations. Considering only the strategies 'amplexus' and 'interference':

1. males adopting amplexus enjoy a high probability of inseminating their mate, but suffer high energetic costs and a low rate of encounter with other females.
2. interfering males escape the latter two costs of amplexus, but do not enjoy as high a probability of inseminating the females they meet.

It must be stressed that any one male is capable of adopting any one of these alternative strategies; his behaviour is a flexible response to the conditions he meets in a sexual encounter, i.e. these are conditional alternative strategies. A further consideration of such strategies in newts is given in Chapter 5.3.

In Chapter 3, it was suggested that the sexual behaviour of the red-spotted newt is bimodal, consisting of amplexus and hula display. The results of the experiments reported in Chapter 4 suggest that this species' sexual behaviour is really trimodal, with 'interference' as the third mode. Such a complex system has no known parallels in the order Urodela; indeed, it is difficult to find any analogues in the whole animal kingdom.

| | Alternative strategies: | | |
|--------------------------------------|-------------------------|------|--------------|
| | Amplexus | Hula | Interference |
| Effort required to stimulate female | +++ | ++ | + |
| Rate of encounter with females | + | ++ | +++ |
| Putative energetic cost of courtship | +++ | ++ | + |
| Probability of inseminating female | +++ | ++ | + |
| Resistance to sexual interference | +++ | + | |

Note: The series +, ++, +++ indicates increasing values of a particular variable.

Table 4.6 The costs and benefits of amplexus, hula and interference as alternative mating strategies of male red-spotted newts.

| | Alternative strategies: | | |
|-----------------------------------|-------------------------|----------------|-------------------|
| | Arthropod feeding | Saliva feeding | Forced copulation |
| Probability of sperm transfer | +++ | ++ | + |
| Direction of female choice | +++ | ++ | + |
| Number of eggs fertilized by male | +++ | ++ | + |
| Risk of predation by spiders* | +++ | ++ | + |

Note: The series +, ++, +++ indicates increasing values of a particular variable.

*: Risk is negatively correlated with male size.

Table 4.7 Some of the costs and benefits associated with the alternative mating strategies of male scorpion flies of the genus *Panorpa*. Derived from data in Thornhill (1981).

Perhaps the closest analogue is the scorpion fly genus *Panorpa*, mentioned briefly in Chapter 3.6. In these insects, males either feed their mates with arthropods found in spider-webs, feed them with salivary secretions or attempt to forcibly copulate with them. The male decides which strategy to opt for on the basis of his size and the availability of arthropod prey. Thornhill (1981) has analyzed these alternative mating strategies in terms of their costs and benefits, stressing that these are conditional strategies. Some of his data are summarized in Table 4.7. Large males benefit the most from feeding their mates arthropod prey; for smaller males, foraging for such items is risky, and many adopt one or other of the two strategies involving a low probability of sperm transfer. Thornhill (1981) argues that in these flies a male's reproductive success is largely unpredictable, and that this has selected for a flexible set of conditional alternative strategies.

Thornhill's data are especially satisfying because they are derived from field observations, and field and laboratory experiments. The data for the red-spotted newt are solely derived from laboratory experiments. Some field data relevant to this latter species are discussed in Chapter 5.2.1.

CHAPTER 5

CHOICE AND COMPETITION: PLACING
NEWS IN CONTEXT

CHAPTER 5

CHOICE AND COMPETITION: PLACING NEWTS IN CONTEXT

In this Chapter, mate choice and male competition in the smooth newt and the red-spotted newt are considered as coevolutionary arms races, one between males and females, the other between males and males (Dawkins and Krebs 1979).

In Chapter 5.1, mate choice is discussed as a race between males and females. In Chapter 5.2, the competitive race between males is considered at the behavioural, ecological and physiological levels. Sexual interference by female mimicry is considered as an alternative male strategy in Chapter 5.3, together with some examples of mimicry in other animals. Chapter 5.4 considers the evolution of urodele sexual behaviour and the phylogeny of the salamandrids and in Chapter 5.5, some areas for further research are outlined.

5.1 Courtship Behaviour and Mate Choice: an Arms Race between Males and Females

The functions of mating behaviour were classified by Tinbergen (1953) as:

1. Reproductive isolation, ensuring that only individuals of the same species mate with one another.
2. Synchronization between the male and female in the timing of mating.
3. Orientation in space such that the male can locate and inseminate the female.
4. Persuasion, in which the male stimulates the female to mate.

A fifth function of mating behaviour, not included in Tinbergen's list, can be added:

5. Assessment of a conspecific as a suitable mating partner (Trivers 1972).

In this section, each of these functions of sexual behaviour is discussed in the light of the data presented in this thesis for the smooth newt and the red-spotted newt.

5.1.1 Reproduction Isolation

The role of sexual behaviour in reproductive isolation between related species of newts has been poorly studied. No data are available for the red-spotted newt, and only very few for the smooth newt. In the latter, a number of features of the male's courtship display show interspecific differences. For instance, the speed at which the male fans his tail during the static display stage of an encounter is lower in *Triturus vulgaris* than in *T. helveticus*, the palmate newt (Halliday 1977a).

Similarly, the posture adopted by the male whilst displaying to the female is slightly different in these two species (van Gelder 1979). However, there is no evidence to support the notion that these differences form effective premating barriers to interspecific mating. This subject is currently under investigation (J.M. Roberts, in progress).

The secondary sexual characteristics of the male smooth newt suggest an influence of sexual selection, as Darwin (1871) himself recognized. However, there is no evidence that they play any specific role in either mate choice or male competition. It is possible that they function more in terms of reproductive isolation, perhaps in species recognition by the female. There is no empirical evidence to support this view; however, circumstantial evidence is perhaps afforded by the observation that the male smooth newt's secondary sexual characteristics are most sharply delineated from those of the males of related species in those areas where the species are sympatric (see Arnold and Burton 1978).

5.1.2 Synchronization

Synchronization in the timing of mating is especially important in those animals in which fertilization is external. It is nevertheless also important in internally fertilizing animals. The synchronization of male and female behaviour is clearly illustrated by Halliday's work on the causal mechanisms involved in smooth newt courtship (reviewed in Halliday 1977a). Because the male normally only proceeds from one stage in an encounter to the next if the female behaves in an appropriate manner, the partners cannot get 'out of phase' with one another.

In the red-spotted newt, amplexus affords the male such a physical monopoly of the female that asynchrony is impossible. For hula display

and spermatophore transfer behaviour, the 'meshing' of the partners' behaviour is similar to that seen in the smooth newt.

5.1.3 Mate Location and Orientation

In both species of newt, the first meeting of a male and female usually seems to occur by chance; thus mate location is probably not an important aspect of newt courtship. A number of aspects of spermatophore transfer behaviour can be understood in terms of the orientation of the female to the male's spermatophore. For instance, the visual stimuli of the male red-spotted newt's cloacal papillae and odours from his cloacal glands may serve to orient the female. Some form of orientation would be expected given that sperm transfer is external in the urodeles.

5.1.4 Persuasion

Tinbergen (1953) developed the concept of persuasion in view of the fact that the sexual behaviour of many animals is characterized by three conflicting tendencies in the partners; to flee, to attack and to mate (Morris 1956 developed this idea further to produce the FAM theory for the motivation of sexual behaviour.)

It is a general observation that males seem to be far more ready to court females than females are to respond. As discussed in Chapter 1 this is a consequence of the fact that, whereas male fitness is limited by the quantity of females available for mating, female fitness is limited more by quality of mates. This led Williams (1975) to compare males with 'eager salesmen' and females with 'reluctant buyers'. Adaptations in males resulting in greater powers of persuasion, such as more effective courtship display, will result in counter-adaptations in females towards greater

'recalcitrance', ensuring that they mate only with the 'best' males. The outcome of this male-female coevolution may be a run-away escalation, or 'arms race' (Dawkins and Krebs 1979), leading to the evolution of elaborate and complex, stimulatory courtship displays in males, and coyness and choosiness in females.

The mechanisms whereby males stimulate females and attempt to persuade them to mate are legion. Most of Tinbergen's examples of persuasion are in the context of appeasement behaviour, which indicates to the female that the male is sexually motivated and will not attack her. Although female newts do flee from males, the FAM theory is of little relevance to these animals, for they do not attack one another. Nevertheless, much of the courtship behaviour of newts can be thought of as persuasive in function.

In the smooth newt, the male displays to the female with three types of tail movement. The 'wave' is believed to stimulate the female visually, the 'fan' olfactorily and the 'whip' tactually (Halliday 1974). These aspects of the male's display may have a cumulative stimulatory effect on the female. The probability that the female will pick up a spermatophore increases as more sequences are completed in an encounter, i.e. as the amount of stimulation received by the female increases (Halliday 1974). This correlation between stimulation and pick up success does not prove a cause-effect relationship, but may be evidence for a persuasive function of male display behaviour. As discussed below, this order effect can also be interpreted functionally as a form of mate choice.

Direct evidence of a persuasive effect of male behaviour is better in the red-spotted newt. A male will initiate amplexus with an unresponsive female and subject her to a barrage of display actions which serve to stimulate her olfactorily, with cloacal and genial gland secretions, and tactually. Females are more likely to elicit spermatophore deposition from

and be inseminated by males which perform the greatest number of display actions during amplexus. This suggests that the male's behaviour and his glandular secretions have a persuasive or aphrodisiac effect on his mate, raising her sexual responsiveness (Arnold and Houck 1982).

This persuasive function of male sexual behaviour is mediated chemically in many animals (Arnold and Houck 1982); it should be noted that in urodeles, chemical signals, perhaps different from persuasive odours, may also play a role in species recognition and, perhaps, orientation. The males of many species of newts and salamanders develop specialized areas of glandular tissue during the breeding season, often located on the head and in the cloaca. During amplexus in the red-spotted newt, the glands on the male's head are applied directly to the female's snout and cloacal gland secretions are wafted forwards by the vibration of the male's tail. In the smooth newt, cloacal and skin odours are water-borne, directed towards the female by the fanning action of the male's tail. Chemical delivery reaches its most bizarre form in some terrestrial salamanders. For instance, in the plethodontid *Desmognathus ochrophaeus*, the male pulls his head against the dorsum of the female. His premaxillary teeth abrade her skin and secretions from a gland on the male's chin, the mental gland, are rubbed onto the wound. Arnold and Houck (1982) suggest that this behaviour may 'inoculate' the female with an aphrodisiac. However, insemination success appears not to be influenced by removal of either the male's teeth and/or mental gland. Perhaps a more subtle index of persuasion, such as latency to insemination, is required in this instance.

Thus much of the sexual behaviour of newts and salamanders, including *N. viridescens* and *T. vulgaris*, can be understood as a means whereby the male renders his partner fully responsive. Maximal female responsiveness is important if sperm transfer, which is external in newts, is to be successful. As a consequence, sexual selection will favour the evolution

of stimulatory and often complex displays in males, and greater resistance to male displays in females, ensuring that they only mate with males of the highest quality.

5.1.5 Mate Choice

Mate choice can be operationally defined as any behaviour shown by individuals of one sex that leads to their being more likely to mate with certain members of the opposite sex than with others (Halliday 1983). However, before any detailed discussion of this topic, it must be stressed that the experiments on mate choice reported in this thesis were conducted under artificial, laboratory conditions; although the evidence is suggestive of specific mating preferences in males and females, mate choice in the natural environment cannot be taken for granted.

What is the evidence for mate choice in female newts? In the smooth newt, the order effect in success of spermatophore pick up makes it more likely that the female will be inseminated by males capable of producing large numbers of spermatophores, i.e. more fertile males (Halliday 1983). Clearly, this satisfies the operational definition of mate choice given above, but as discussed in the context of persuasion, the mechanism by which the order effect is produced is less clear. Is it the result of a cumulative stimulatory effect of male courtship, or has it evolved as a specific mating preference?

Although female red-spotted newts do not show the order effect, they tend to be mated by males capable of performing the greatest number of display actions during amplexus. Once again, are females actively choosing these males as mates, or is this a motivational effect, with more display resulting in greater persuasion?

Clearly, in these cases mate choice and female motivation have become confounded, and as Halliday (1983) stresses, such a complication arises in many studies of mate choice. For instance, males of the otitid fly *Physiphora diminuta* perform a complex and highly variable courtship display, and sometimes a female will flee from a displaying male. Alcock and Pyle (1979) suggest that the male's display advertises his physiological condition, and thus his genetic 'quality'; when a female flees, she is rejecting the male as an unsuitable mate. These authors do not, however, discuss the alternative hypothesis for why females flee: that they are not sufficiently persuaded to copulate.

In the smooth newt, the female seems to prefer males reasonably well matched to herself in body length, i.e. there is a size-assortative preference. Such a preference may be adaptive if the probability of sperm transfer increases as the partners become more matched in length. Although untested, this hypothesis seems plausible given that, after spermatophore deposition, the male moves forwards one body length and is followed by the female (Halliday 1974). If this preference exists in the field, it cannot be explained in terms of female persuasion.

Male newts of both species appear to prefer larger, more fecund females as mates, a preference not uncommon in the animal kingdom, especially in those species in which males invest heavily in their offspring. For instance, it is found in those species in which males transfer nutrients as well as sperm at mating (Gwynne 1981) or provide paternal care (Downhower and Brown 1981). However, as male newts do not seem to invest particularly heavily, why are they choosy?

In causal terms, it is possible that such choice occurs because larger females represent a particularly strong sexual stimulus. A functional interpretation can also be advanced. In the red-spotted newt,

it is known that sperm is a limited resource; the male begins each breeding season with a finite supply and does not produce any more mature sperm until after the end of the season (Adams 1940). Given the similarities in life history and close taxonomic affinity between the red-spotted newt and the smooth newt, sperm may be limited in the latter species also. This limitation may greatly reduce the reproductive potential of the male, for each mating depletes an already-limited supply of sperm. It seems likely that this could favour mate choice, and given that female body size is a reliable indicator of female fecundity in many urodele species (Kaplan and Salthe 1979), choice for large females is not surprising.

In addition to an apparent preference for larger females, the male smooth newt requires more tail touches from the female in order to elicit spermatophore deposition as more sequences are completed in an encounter (Halliday 1976); he seems to raise the criterion for deposition, requiring that his partner responds in a more strongly positive way as the encounter proceeds. The male thus appears to be 'testing' the female's responsiveness which, as suggested above, is probably influenced by the degree to which his courtship display stimulates her. In effect, this behaviour on behalf of the male may safeguard against depositing large numbers of spermatophores with a female insufficiently responsive for successful sperm transfer (Halliday 1977a), a form of mate choice which would seem to be of obvious value given that the male's supply of sperm is probably limited.

If the size preferences which male and female smooth newts show in the laboratory are also shown in the field, then it seems possible that, at least occasionally, sexual encounters may show an element of male-female conflict. In the extreme case, a male should reject all but the largest females that he meets (females which will be equally valuable to all males), whereas females should reject all males except those best matched in size (males which will be valuable only to the females that they match). Thus,

encounters between large males and large females should contain the least conflict, for the mating preferences of both partners will be satisfied. Similar conflicts over mating decisions occur in other animals; for instance, in the common toad *Bufo bufo*, there is a conflict over mate size (Davies and Halliday 1977), although mate choice may be of little importance in this species. In the yellow-bellied marmot, *Marmota flaviventris*, males attempt to mate polygynously by amassing a harem, whereas females attempt to mate monogamously (Downhower and Armitage 1971). Clearly, reproduction cannot be regarded as an activity in which males and females necessarily behave in a way that maximizes their mutual benefit.

Janetos (1980) has used computer simulation to consider the ways in which animals should behave so as to choose the most fit individuals for their mates. He has produced four models of mate choice:

1. random mating.
2. mating with an individual whose 'quality' exceeds some threshold, but mating with a sub-threshold individual if time becomes limited.
3. a one-step decision process, in which the threshold is reduced as time becomes limited.
4. sampling n individuals, and mating with the best of them.

Under simulation, random mating yields the worst return and sampling n individuals the best return in terms of mate fitness. Given a lack of field data, it is difficult to suggest the possible mechanism by which newts choose their mates. On the basis of the laboratory data presented in this thesis, random mating seems unlikely. Sampling n individuals assumes that the newt can remember the position of the best individual and has time to choose; as newts tend to be quite mobile, especially males, this model is perhaps untenable. The second and third models may be

applicable, but once again, male choice and female motivation can become confounded. T.R. Halliday (personal communication) notes that in both of these models, females become less choosy over time. Such might be the case if, at the beginning of the breeding season, female motivation is so low that only the most effective courtship displays will persuade her to mate. Her 'choice threshold' thus appears to be high. However, as the season progresses, the female may be subjected to many unpersuasive displays which, nevertheless, 'prime' her motivationally. As this priming effect becomes stronger, the female may respond to even the most unpersuasive males, having apparently relaxed her criterion of mate choice.

Such priming effects of male courtship are known to occur in a number of animals. For instance, female green anoles (*Anolis carolinensis*) will only show complete ovarian recrudescence if courted by males early in the breeding season, even though these courtships do not lead to mating (Crews 1980). Similarly, female pomacentrid fish (*Chromis cyanea*) are courted by many males before they finally mate and it seems that it is the cumulative effect of all this courtship, rather than any aspect of the male with which she finally mates, that determines when the female mates (de Boer 1981). Of course, as far as newts are concerned, a priming effect of courtship is mere speculation, although it is true that females will sometimes engage in a number of incomplete courtships before finally becoming inseminated. What this speculation indicates is the need for further investigation and the need for care in interpreting what seems to be evidence of mate choice. This evidence may sometimes be more parsimoniously explained on the basis of differences and changes in female motivation.

Of course, mate choice, when it occurs, can be based on multiple criteria. In newts, such criteria appear to include morphological and behavioural characteristics, e.g. size, responsiveness and effectiveness

of courtship display. Mate choice based on multiple criteria has been studied in few species; one notable study is that of Burley (1981), who has found that plumage colour, social rank, age and breeding experience determine mate preferences in the pigeon, *Columba livia*. Once again, further investigation of newts is indicated.

5.1.6 Choice and Competition.

Whether females actively choose their mates or, more passively, simply respond to more effective courtship displays, males will compete for them. Despite the heuristic value of separating choice from competition, they are not alternative ways by which variance in mating success may be produced. Within a species, indeed within a sex, both may be acting simultaneously, one sometimes facilitating or inhibiting the other (Halliday 1983).

The nature of the interactions between choice and competition in newts has not been systematically investigated, but a number of questions pose themselves. If large females are equally valuable to all males, is sexual interference more likely if the female is larger than if she is small? Under the threat of sexual interference, do male red-spotted newts clasp any female regardless of her size, for, after all, it may be better to settle for a suboptimal female than risk losing access to all females through being too choosy?

The only data relevant to the question of how choice and competition interact are those in Chapter 2.4, where it was shown that female smooth newts seem to prefer their males one at a time. It was suggested that this preference may result from the fact that sexual interference by female mimicry may render the female unable to effectively choose her mate and be inseminated by him. If this interpretation is correct, then

it suggests a negative interaction between choice and competition in the smooth newt.

5.1.7 Summary

The sexual behaviour of newts appears to fulfill at least some of the general functions of sexual behaviour suggested by Tinbergen (1953). Although the role of behaviour in reproductive isolation has yet to be fully explored, the male and female would gain a mutual benefit by avoiding interspecific mating leading to the production of unfit, hybrid offspring.

However, because males are always willing to mate, but females are not always responsive towards males, there may arise a conflict, or arms race, between the sexes. Selection will favour the evolution of more effectively persuasive male courtship displays, as occur in both the smooth newt and red-spotted newt. Similarly, selection will favour greater recalcitrance, or resistance to males, in females. Much of the sexual behaviour of male newts, indeed of male animals in general, can be understood as an attempt to persuade females to mate, an attempt to alter female motivation. When females respond differentially towards males, it is not always possible to determine whether this is due to differences in female motivation or active mate preferences. Perhaps preferences for mates of certain sizes are the best evidence for active choice, unconfounded by motivational effects, in newts.

It may thus be more parsimonious to explain apparent mate choice on the basis of female motivation and male persuasion. However, both mate choice and motivation will have the same net result, that is differential male mating success. As discussed in the next section, differential male

mating success may be produced by interactions between males as well as by interactions between males and females.

5.2 Competition: An Arms Race between Males

5.2.1 Behavioural and Ecological Aspects

In the last section, it was suggested that beneath the apparent mutualism of mating in newts there are conflicts of interest, and that male and female sexual strategies are better regarded as an arms race. However, the arms race concept in newts is most obvious in terms of competitive interactions between males, for as mechanisms of 'attack' become more efficient, so selection will favour better mechanisms of 'defense'. Although in this context the word 'attack' does not necessarily imply physical assault, this type of co-evolution has been termed an attack-defense arms race (Dawkins and Krebs 1979).

There are five types of male competition in the order Urodela (Arnold 1977), and these, together with all of the species that show them, are listed in Table 5.1.

The five types consist of:

1. profuse spermatophore production, in which the male deposits large numbers of spermatophores in the vicinity of the female. This behaviour is a form of extra corporeal sperm competition (Parker 1970), for it may increase the probability that the female will pick up one male's sperm rather than those of another. However, Arnold (1977) has noted that this type of behaviour occurs most often in explosively breeding species, and suggests that it may be a consequence of compressing a breeding season's reproductive effort

| Species | Profuse Spermatophore production | Spermatophore covering | Female Mimicry | Displacement during amplexus | Overt fighting | References |
|--------------------------------------|--|---------------------------|-------------------|------------------------------------|-------------------|----------------------------|
| <i>Triturus vulgaris</i> | | | ✓ | | | This thesis |
| <i>Notophthalmus viridescens</i> | | | ✓ | ✓ | | This thesis |
| <i>Taricha</i> spp. | | | | ✓ | | Ritter 1897, Smith 1941 |
| <i>Pleurodeles waltlii</i> | | | | ✓ | | Arnold 1977 |
| <i>Ambystoma annulatum</i> | ✓ | ✓ | | | | Spotila & Beumer 1970 |
| <i>A. maculatum</i> | ✓ | ✓ | | | | Arnold 1976 |
| <i>A. opacum</i> | | ✓ | | | | Arnold 1972 |
| <i>A. mexicanum</i> | | ✓ | | | | Arnold 1972 |
| <i>A. tigrinum</i> | | ✓ | ✓ | | | Arnold 1976 |
| <i>A. laterale</i> | | | | ✓ | | Storez 1969 |
| <i>A. macrodactylum</i> | | | | ✓ | | Anderson 1961 |
| <i>A. jeffersonianum</i> | | | | ✓ | | Kumpf & Yeaton 1932 |
| <i>A. texanum</i> | ✓ | ✓ | | | | Gorton 1972 |
| <i>Rhyacotriton olympicus</i> | | | | | ✓ | Arnold 1972 |
| <i>Desmognathus ochrophaeus</i> | | | | | ✓ | Organ 1961 |
| <i>Pseudotriton ruber</i> | | | ✓ | | ✓ | Organ & Organ 1968 |
| <i>Eurycea bislineata</i> | | | | | ✓ | Arnold 1972 |
| <i>Aneides aeneus</i> | | | | | ✓ | Cupp 1980 |
| <i>Plethodon jordani</i> | | | ✓ | | ✓ | Organ 1958, Arnold 1976 |
| <i>P. ouachitae</i> | | | ✓ | | ✓ | Arnold 1972 |
| <i>P. welleri</i> | | | | | ✓ | Organ 1960 |
| <i>P. caddoensis</i> | | | | | ✓ | Arnold 1972 |
| <i>P. glutinosus</i> | | | | | ✓ | Wells 1980 |

Table 5.1 Types of intermale competition which occur in the Urodela.

into a relatively short period of time. Similar behaviour occurs in a number of arthropod species with external sperm transfer (Cloudsley-Thompson 1976).

2. Spermatophore covering, in which the male places his spermatophore on top of that of another male. Only the uppermost spermatophore is available to the female. Once again, this can be regarded as a form of sperm competition. Spermatophore covering is not known in any other animal group; however, in the pseudoscorpions, a male that finds another's spermatophore will destroy it and replace it with one of his own (Weygoldt 1966).
3. Female mimicry, in which the male mimics female behaviour in order to usurp a male already engaged in courtship. The mimicking male then attempts to inseminate the female himself.
4. Displacement during amplexus, in which the male attempts to displace an amplexant male in order to take-over the female and inseminate her himself. Similar behaviour occurs during mounting and copulation in many arthropods (Parker 1974), and during amplexus in many anuran amphibians (Wells 1977).
5. Overt fighting, which may consist of chasing, biting and threatening, and may occur in the context of territoriality. Fighting is the most obvious and most common type of male competition in animals (Wilson 1975).

As indicated, none of these types of competition are unique to the order Urodela, and all can be placed in the context of the major types of competition shown by animals which are listed in Table 1.1. Despite the small number of urodele species for which data are available, Table 5.1 reveals a number of broad taxonomic trends. For instance, spermatophore covering seems to be characteristic of the ambystomatid salamanders; in

Ambystoma tigrinum, female mimicry enables the male to cover another's spermatophore (Arnold 1976). Similarly, overt fighting seems to be more or less restricted to the terrestrial plethodontid salamanders, a family which also contains a number of species that show territorial and female mimicry behaviour. These examples also demonstrate that more than one of the five types of competition listed can be exhibited by a single species.

In the family Salamandridae, competition has only been described for the genera *Taricha* and *Pleurodeles*. In both, courtship includes a period of amplexus, during which the amplexant male is vulnerable to attempted displacement from unpaired males. This type of competition also occurs during amplexus in *Notophthalmus*, although such attempts appear to be seldom successful at displacing the courting male. After the male red-spotted newt dismounts from the female, he is vulnerable to sexual interference by female mimicry. Although this does not decrease the probability of the male inseminating his mate, it does sometimes result in the interfering male also inseminating the female. This type of sexual interference also occurs during hula encounters in the red-spotted newt, but is more frequent. However, hula encounters seldom occur in the presence of rival males as there is a shift to amplexus under these conditions, regardless of the female's initial responsiveness. Males which switch to amplexus in the presence of rivals remain clasped to the female for longer if the rivals attempt displacement. In this respect, amplexus seems to function as a form of sexual defense, a counter adaptation to the activities of other males in the competitive arms race. As suggested in Chapter 4, it also serves another purpose, that is to enable the male to capture an unresponsive female and, with his display, render her sufficiently responsive for sperm transfer. It is not clear whether amplexus in the red-spotted newt evolved primarily as a mechanism of sexual defense or as a mechanism for making females responsive; selection would have favoured amplexus whatever its initial function.

As a form of mate guarding, amplexus in the red-spotted newt resembles the physical mate guarding behaviour of many other animals, especially arthropods (Parker 1970, 1974). In many insects and crustaceans, males mount females sometime before actual sperm transfer occurs, and guard them from the advances of other males, e.g. the amphipod *Gammarus pulex* (Birkhead and Clarkeson 1980) and the isopod *Asellus aquaticus* (Ridley and Thompson 1979).

Sexual interference by female mimicry also occurs in *Triturus vulgaris*. In this species, it does decrease the chances of the courting male inseminating the female, and may also result in the rival inseminating her. In the smooth newt, there is no amplexus with which the male can monopolize his mate. Instead, he attempts to draw her away from the rival by increasing the duration of his periods of retreat display. He also displays to the female in the initial, static display phase of an encounter at a greater intensity, which may serve to so motivate her that she ignores other males in the vicinity. Once again, the male's behaviour seems to have evolved to serve two different functions, defense against rivals and rendering the female responsive.

Sexual interference by female mimicry has been observed in only a few urodele species, but these represent all three major urodele families (see Table 5.1). Arnold (1977) has noted the general similarities between most genera in the spermatophore transfer stage of courtship, and it thus seems probable that this type of competition is quite common in the urodeles, the exploitation of a weak link in the courtship sequence.

The intensity of male competition within a breeding population will be influenced by the ratio of sexually active males to responsive females at any one time, a measure known as the operational sex ratio, or OSR (Emlen and Oring 1977; Wade and Arnold 1980). For most urodele species,

only data on overall adult sex ratios are available; however, given that the potential for multiple mating is probably greater in males than females (Halliday and Verrell 1983), the OSR is likely to be skewed towards an excess of males in many species.

Table 5.2 presents data on sex ratios in breeding populations of nine aquatic-breeding urodele species. In most, the sex ratio is skewed towards an excess of males. In seven species, OSRs are likely to be even more skewed due to the fact that males remain at the breeding site for longer than females. For instance, in the salamander *Ambystoma jeffersonianum*, a species in which unpaired males attempt to displace those in amplexus (Kumpf and Yeaton 1932), there are about two males for every female over the course of the breeding season. However, daily OSRs vary between 2.7 and 10.1 males per female, due to the shorter residency of individual females at the breeding pond (Douglas 1979).

Sex ratios are difficult to estimate in those salamanders that breed on land, because populations are not spatially confined in many species. In the terrestrial plethodontids, sex ratios range across species from approximately equal numbers of males and females, e.g. *Plethodon glutinosus* (Wells 1980) to an excess of males, e.g. *P. jordani* (Arnold 1976). In those salamander species which are territorial, sex ratios may be skewed towards an excess of females in areas where males take up residence (Halliday and Verrell 1983).

In the red-spotted newt, males remain at the breeding site for longer than females, and adult sex ratios tend to be skewed towards an excess of males (Table 5.2). At first glance, this suggests that the OSR in this species will be male-skewed; however, the concept of the OSR is not clear cut in the red-spotted newt, because initially unresponsive females can be rendered responsive by the male's behaviour during amplexus. In the

| Species | Sex ratio | Males stay longer than females | References |
|----------------------------------|---|--------------------------------|--|
| <i>Ambystoma jeffersonianum</i> | 2.3, 2.7 ^a | + | Douglas (1979) |
| <i>A. talpoideum</i> | ca. 1.0 | + | Hardy & Raymond (1980) |
| <i>A. maculatum</i> | 1.87 | + | Husting (1965) |
| <i>A. annulatum</i> | > 1.0 | + | Spotila & Beumer (1970) |
| <i>Taricha torosa</i> | > 1.0 | + | Smith (1941) |
| <i>T. rivularis</i> | ca. 5.0 ^b | + | Hedgecock (1978) |
| <i>Triturus cristatus</i> | 1.28, 1.72 ^c . ca. 1.0 | ? | Hagstrom (1979) Bielinski (pers. comm.) |
| <i>T. vulgaris</i> | 0.78, 1.52 ^d . < 1.0 | ? | Hagstrom (1979) Bell (1977) |
| <i>Notophthalmus viridescens</i> | > 1.0 > 1.0 ca. 2.0 4.7 - 1.6 ^e | + | Hurlbert (1969) Bellis (1968) Gill (1978a,b) |

All ratios are expressed as number of males/number of females.

- a Data for two different years.
- b Data for 1955.
- c First value = estimated for population, second value = ratio for recorded animals.
- d Data from several populations
- e First value = spring breeding season, second value = autumn breeding season.

Table 5.2 Data on the overall sex ratio in breeding populations of aquatic-breeding urodeles.

smooth newt, adult sex ratios vary from an excess of one sex to an excess of the other, suggesting some variability in OSR. Male smooth newts have been described as showing some degree of home range fidelity in the breeding pond (Dolmen 1982); however, it is not clear whether the males might be defending resources, such as food patches, or display areas, as on a lek (Emlen and Oring 1977). A. Bielinski (unpublished data) has evidence, derived from trapping records, that males move quite freely around their pond, and the question of newt home range is thus an open one. In all, however, it seems that the ecological conditions favouring male competition are observed in at least some populations of both species of newt.

5.2.2 Physiological Aspects: Sperm Competition

In many animals, the arms race between males does not stop at insemination. The race can be thought of as a competition to fertilize a female's ova and thus when a female is inseminated by two or more males, their sperm may compete with one another in the female's genital tract (Parker 1970, 1983). This idea of sperm competition was raised earlier, when it was suggested that the profuse production of spermatophores and spermatophore covering can be thought of as cases of extracorporeal sperm competition. Concerning sperm competition within the female's genital tract, Halliday and Verrell (1983) have reviewed those aspects of urodele reproductive biology which are relevant to such competition and conclude that there are good grounds for expecting it to occur in these animals. In this section, those aspects relevant to sperm competition in newts are considered.

Sperm competition is only possible if female newts are inseminated by more than one male. Female smooth newts and female red-spotted newts may be multiply inseminated as a consequence of sexual interference by

female mimicry (first the courter, then the rival), and due to remating before (both species) and after (the red-spotted newt) the onset of oviposition.

The sperm of different males must remain in the female's genital tract at the same time if sperm competition is to occur. Female urodeles store sperm in a specialized cloacal structure known as a spermatheca. In *Notophthalmus*, the spermatheca consists of a number of short, blind tubules which open into the roof of the cloaca (Dent 1970). The spermatheca of the smooth newt seems to be similar in structure (J.M. Roberts, unpublished data).

The storage of sperm is obviously only of use if the gametes remain viable between the times of insemination and fertilization; in newts, the ova are fertilized as they pass through the cloaca at the time of oviposition (Boisseau and Joly 1975). In the red-spotted newt, sperm may be stored, in a viable state, for several months (D.M. Sever, personal communication), and may be nourished by secretions produced by the epithelial cells lining the spermathecal tubules (Dent 1970). Preliminary investigation of female smooth newts outside of the breeding season has failed to detect the storage of viable sperm (J.M. Roberts, unpublished data), although storage within the breeding season has yet to be studied.

Finally, the competitive ability of a male's sperm may be strongly influenced by the efficiency with which the female stores and uses it. Thus the number of sperm that the female expels onto an egg or batch of eggs may affect the course of sperm competition. Nothing is known about such efficiency in the urodele amphibians.

It thus seems quite possible that sperm competition occurs in newts (see Table 5.3). Assuming that it does occur, it is impossible to predict

| | Red-spotted newt | Smooth newt |
|--|---------------------|----------------|
| Do females mate with more than one male? | Yes | Yes |
| Do females store sperm? | Yes | Yes* |
| Does stored sperm remain viable? | Yes | ? |
| Are sperm used efficiently? | ? | ? |

*On the basis of the fact that females have
organs for storing sperm.

Table 5.3 Aspects of the reproductive biology
of newts which are relevant to sperm
competition.

the exact nature of sperm competition in these animals. In general, sperm competition takes one of three forms (see Parker 1970; Walker 1980) :-

1. the first male to mate fertilizes most of the females ova (priority),
2. the last male to mate fertilizes most of the female's ova (displacement),
3. the sperm from different males mix; paternity depends upon the amount of sperm transferred by each male (mixing).

In both species of newt, sexual interference by female mimicry can result in multiple insemination. Assuming that this type of competition is a specific adaptation, it also seems reasonable to assume that the interfering male gains some benefit from inseminating an already inseminated female. By implication, such a benefit would be in terms of sperm competition, which would seem to be of either the displacement or mixing types. If such is indeed the case, then the sexual interference - defense arms race in newts may be best regarded, at least in part, as a coevolving strategy for precipitating and avoiding sperm competition.

5.3 Sexual Interference by Female Mimicry as an Alternative Male Mating Strategy.

There are numerous examples in the animal kingdom of species in which males interfere with one another's attempts to inseminate females already engaged in sexual behaviour, or sexual interference (Arnold 1976). Here, I consider several aspects of sexual interference achieved by female mimicry.

Female mimicry can be defined as the adoption by a male of the behaviour and/or morphology of conspecific females in such a way that he gains access to females. In some species, female mimicry enables the male to gain access to resources needed by females for successful reproduction, e.g. kleptoparasitic female mimicry in the scorpion fly *Hyllobittacus apicalis* (Thornhill 1979). In others, it enables young males to avoid aggression from older males and establish breeding territories, e.g. plumage mimicry in many sub-adult passerine birds (Rohwer, Fretwell and Niles 1980).

Sexual interference by female mimicry has evolved in all three major urodele families (see Table 5.1). Some examples of this behaviour in other animal species are listed in Table 5.4. It seems to be especially common in the bony fishes in which the typical male sexual strategy is to defend a nest-site, attract females to it for mating and then guard the eggs and fry. By appearing as conspecific females, female mimics intrude on mating pairs and attempt to fertilize at least some of the eggs which the nest-owner will subsequently guard. In some species, such as the bluegill sunfish, female mimicry may be a pure, genetically-determined strategy (Dominey 1980). In others, female mimicry is a conditional strategy adopted by males which are too small to compete successfully with larger males, e.g. the gila top-minnow (Constantz 1975).

In the sticklebacks (see Table 5.4), female mimicry is conditional on the male encountering a female already engaged in courtship; even a nest-owner will temporarily become a female mimic in order to interfere with the courtship of a neighbour.

The sticklebacks are perhaps the fishes most similar to the newts in terms of female mimicry. In both the smooth newt and the red-spotted newt, the male will court a female if she is alone, and sexually interfere if

| Species | References |
|---|--|
| <i>Photinus macdermotti</i> , a firefly | Lloyd (1979) |
| <i>Gasterosteus aculeatus</i> , the three-spined stickleback | van der Assem (1967) |
| <i>Apeltes quadracus</i> , the four-spined stickleback | Rowland (1979) |
| <i>Pygosteus pungitius</i> , the ten-spined stickleback | Morris (1952) |
| <i>Tripterygion</i> spp, Mediterranean blennies | Wirtz (1978) |
| <i>Polycentrus schomburgkii</i> , the leaf fish | Barlow (1967) |
| <i>Poeciliopsis occidentalis</i> , the gila topminnow | Constantz (1975) |
| <i>Lepomis macrochiris</i> , the blue gill sunfish | Dominey (1980) Gross & Charnov (1980) |
| <i>Anolis garmani</i> , a Jamaican lizard | Trivers (1976) |
| <i>Iguana iguana</i> , the green iguana | Dugan (1980) |

Table 5.4 Some examples of species in which female mimicry is used in the context of sexual interference.

if she is already being courted. Adopting the behaviour of a conspecific female, the mimic interferes at the most crucial and most vulnerable stage in a sexual encounter, when the courting male has turned away from the female to deposit a spermatophore. Sexual interference by female mimicry is thus a conditional alternative mating strategy in newts.

Dunbar (1982) suggests a category of conditional strategy known as a 'side-payment strategy', in which an individual opportunistically collects whatever gains are to be obtained 'on the side' from a subsidiary strategy, whilst pursuing a primary, high gain strategy. 'Gain', of course, should be measured in units of fitness. In both species of newt, courtship is the primary, high gain strategy, whereas sexual interference is the subsidiary strategy with lower gain. Newts thus seem to follow a side-payment strategy and, in these animals, probability of sperm transfer is the most easily quantified measure of gain. However, it must be remembered that the correlation between sperm transfer and fertilization success, a better measure of partial fitness, may be weakened by sperm competition.

5.4 The Evolution of Sexual Behaviour in the Salamandrid Urodeles.

Towards the end of the Palaeozoic era, probably in the Devonian period, the first tetrapods appeared on land, derived from rhipidistian or dipnoan fish ancestors. By about 225 million years ago, the order Urodela had arisen from ancestral stock and by the late Jurassic or early Cretaceous periods of the Mesozoic era, the urodeles had radiated into their presently known families (Naylor 1980). The sexual behaviour of these animals has thus had at least about 225 million years in which to evolve into that which we observe today.

Because animal behaviour does not fossilize, it is risky to construct phylogenetic relationships on the basis of similarities and differences in sexual behaviour. Nevertheless, it is my intention to speculate on how the observations reported in this thesis contribute to an understanding of urodele phylogeny and on how the sexual behaviour of these animals may have evolved.

Arnold (1972, 1977) has used sexual behaviour as a diagnostic character for determining evolutionary relationships in the urodeles. He attributes the elaborate courtship rituals of many species to the difficulties associated with indirect sperm transfer by means of a spermatophore, and taxonomic diversity in these rituals to the long evolutionary history of this group. In particular, he points to the diversity of mechanisms by which males render females responsive (see also Arnold and Houck 1982). In many species, the male physically monopolizes the female and, by applying glandular secretions with an aphrodisiac function, alters his partner's motivational state. The red-spotted newt is just such a species. In others, there is very little contact between the male and female; glandular secretions are not directly applied to the female but are carried on water currents generated by the male. Newts in the genus *Triturus*, which includes the smooth newt, are good examples of urodeles with this type of sexual behaviour.

Physical monopolization of the female, ranging from simple close proximity to amplexus, occurs in all three major urodele families, the Plethodontidae, the Ambystomatidae and the Salamandridae; its origins, whether mono- or polyphyletic, are unknown. In all of the species for which sufficient data are available, monopolization serves two functions. First, it enables the male to stimulate the female, and thus alter her responsiveness, and secondly, it enables him to guard his mate against the advances of other males. It is impossible to determine which of these two

functions come first in an evolutionary sense; however, both are clearly favoured by sexual selection.

Competition between males has probably influenced the amount of time that the male invests in each spermatophore he deposits. Lengthy courtships, i.e. greater investment, promote pick-up success, but lay the male open to competition and reduce the time available for other courtship attempts. Not surprisingly, lengthy courtships tend to occur in those species in which the male physically monopolizes the female, and in territorial species. Where the male has no means of monopolizing his mate, courtship is often brief. Arnold (1977) has shown that, in the Ambystomatidae, courtship is rapid in species such as *Ambystoma maculatum* in which there is no amplexus and courtship occurs in dense, polyandrous aggregations, but is more prolonged in species in which there is amplexus, e.g. *A. jeffersonianum*.

The number of spermatophores that the male deposits in an encounter is likely to be a compromise between the minimum number needed to maximize the probability of insemination, and the duration of the breeding season (Arnold 1977). If the season is prolonged, selection may favour those males which conserve some sperm for use later in the season. Thus, in those *Ambystoma* species with short, or explosive, breeding seasons, there is an almost explosive production of spermatophores, whereas in the genus *Plethodon*, with much more prolonged breeding seasons, spermatophore production occurs at a much lower rate. It is also possible that sexual competition has influenced the evolution of patterns of spermatophore production; as discussed in Chapter 5.1, flooding the local environment with spermatophores may enable a male to maximize the chances that a female will pick up his sperm, and not that of another male.

There are about 14 genera in the family salamandridae. Wake and Ozeti (1969) have recognized four groups of genera, based on character analysis of feeding mechanisms. One of these groups (see Figure 5.1) consists of the genera *Euproctus*, *Taricha*, *Notophthalmus*, *Cynops* and *Triturus* (with four others). In the first genus, the male holds the female in amplexus with his tail; in *Taricha*, the male clasps the female with both pairs of his limbs, in *Cynops*, the male clasps the female in a rather weak and variable manner, often merely placing a foot on her dorsum. In all three species, the male is able to stimulate the female whilst restraining her (Halliday 1977a). Amplexus is absent in *Triturus*; instead, the male performs a complex lateral display consisting of three tail movements, some of which stimulate the female with water-borne odours. In *Notophthalmus*, the male's sexual behaviour depends on the initial responsiveness of his mate; if she is unresponsive, he clasps her, but if she is responsive, he performs a relatively simple lateral (= hula) display.

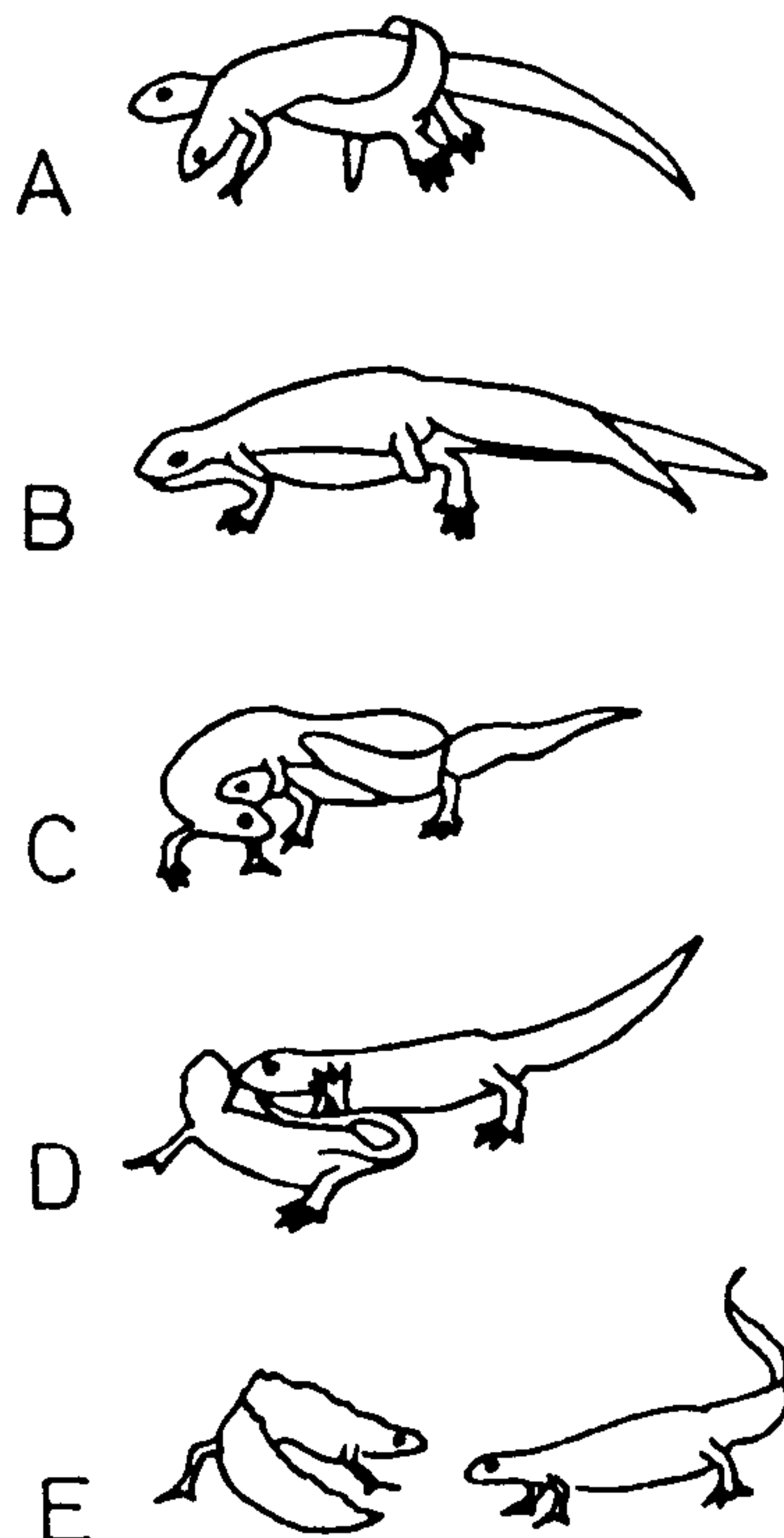


Figure 5.1 Display orientations in five salamandrid genera.
A. *Euproctus*, B. *Taricha*, C. *Notophthalmus*,
D. *Cynops*, E. *Triturus*.

In this respect, the red-spotted newt seems to occupy an intermediate position in the salamandrids, for it has amplexus, like *Taricha* and *Euproctus*, and a lateral display, like *Triturus* (*Cynops* is also somewhat intermediate, with its rather weak amplexus). It is difficult to establish the precise evolutionary relationship of *Notophthalmus* to *Triturus*, although it does appear that the former has specialized in amplexus and the latter in lateral display. One can envisage a number of possible evolutionary scenarios for these two genera. For example:

1. *Triturus* may be derived from a *Notophthalmus*-like ancestor, but may have lost amplexus and elaborated lateral display.
2. Amplexus may be a secondarily-derived character in *Notophthalmus*, evolving under the influence of sexual selection; hula display may once have been as complex as the display of *Triturus*, but may now be a degenerate character, more or less replaced by amplexus.

No doubt other scenarios could be proposed, but my intention here is to indicate the complexity of the area rather than suggest evolutionary routes.

As a final topic for some speculation, it is interesting to ask why there is such a diversity of types of male competition in the urodeles. Why are some species territorial, but not others? Why, if sperm competition does occur (as is likely), do not males guard their mates after insemination? Why don't newts fight? For some of these questions, the answers seem relatively obvious. For instance, territoriality is only adaptive if a particular limited resource is patchily distributed and economically defendable (Wilson 1975) - perhaps that is why plethodontids defend damp, food-rich areas on land, whereas water-breeding urodeles, living in an environment in which food patches are mobile and abundant, do not. Similarly, males might not guard their mates after insemination

because the opportunities missed for further matings in the period leading up to oviposition would outweigh the advantage gained by guarding a single female. It is, of course, far more difficult to determine why certain characters have not evolved than it is to determine why they have.

Throughout this chapter, it has been suggested that there is an arms race between males and females and males and males. The evolutionary origins of such races are uncertain in some respects, but it is clear that this concept does help clarify some issues in terms of urodele sexual behaviour.

5.5 Areas for further investigation.

The results presented in this thesis form part of a continuing study of newt sexual behaviour. All of the experiments described were conducted in the laboratory; this allows precise experimental control, but conditions in the laboratory are obviously very different from those in the field. Given that the behaviour of a species has evolved in the natural environment, one can never be entirely sure that laboratory results accurately reflect the species' natural behaviour.

Given this proviso, a field study of newt behavioural ecology would be extremely valuable, but difficult due to the rather secretive habits of these animals. Observations of sexual behaviour in the field would undoubtedly shed some light on the frequency with which the various alternative strategies of males of both species are adopted. Indeed, it may be possible to conduct field experiments, say, altering sex ratios, in artificial enclosures, e.g. wire baskets partially submerged in ponds. By fully enclosing ponds with drift-fences and pit-fall traps, it should be

possible to provide estimates of operational sex ratio, an important determinant of the intensity of sexual selection.

A number of basic aspects of newt reproductive biology are relevant in a consideration of sexual selection, some of which are amenable to laboratory study, e.g.

1. the metabolic/energetic constraints on courtship, especially for amplexus in the red-spotted newt,
2. the distribution of sperm and spermatophores within individual sexual encounters and over the course of the breeding season,
3. the inter-relationships between initial insemination, oviposition and remating by females,
4. (of more general interest) the annual gonadal cycles of both sexes, especially for the smooth newt.

Sperm competition has yet to be fully investigated in urodeles, but is clearly an important topic if sexual interference in newts is to be properly understood. Halliday and Verrell (1983) have outlined the methodological approaches to studying sperm competition, and much pilot research would be required in order to find a methodology suitable for newts.

It is thus clear, and not too surprising, that as more questions are answered, there are more to ask. Some of these form the basis of a project grant awarded by the Open University to T.R. Halliday and the author, for three years of further research into the ecological, physiological and behavioural factors that control reproductive activity in newts.

CHAPTER 6

REFERENCES

- ADAMS, A.E. (1940) Sexual conditions in *Triturus viridescens*. III. The reproductive cycle of the adult aquatic form of both sexes. *Amer. J. Anat.* 66, 235-275.
- ALCOCK, J. & PYLE, D.W. (1979) The complex courtship behavior of *Physiphora demandata* (F) (Diptera: Otitidae). *Z. Tierpsychol.* 49, 352-362.
- ANDERSON, J.D. (1961) The courtship behavior of *Ambystoma macrodactylum croceum*. *Copeia* 1961, 132-139.
- ARNOLD, E.N. & BURTON, J.A. (1978) *A Field Guide to the Reptiles and Amphibians of Britain and Europe*. Collins, London.
- ARNOLD, S.J. (1972) The evolution of courtship behavior in salamanders. Ph.D. Dissertation, University of Michigan.
- ARNOLD, S.J. (1976) Sexual behavior, sexual interference and sexual defense in the salamanders, *Ambystoma maculatum*, *Ambystoma tigrinum* and *Plethodon jordani*. *Z. Tierpsychol.* 42, 247-300.
- ARNOLD, S.J. (1977) The evolution of courtship behavior in New World salamanders with some comments on Old World salamandrids. In D.H. Taylor & S.I. Guttman (eds). *The Reproductive Biology of Amphibians*. pp. 141-183. Plenum, New York.
- ARNOLD, S.J. & HOUCK, L.D. (1982) Courtship pheromones: evolution by natural and sexual selection. In M.H. Nitechki (ed). *Biochemical Aspects of Evolutionary Biology*. pp. 173-211. University of Chicago Press, Chicago.

ATTAR, E.N. & MALY, E.J. (1980) A laboratory study of preferential predation by the newt *Notophthalmus v. viridescens*. *Can. J. Zool.* 58, 1712-1717.

BARLOW, G.W. (1967) Social behavior of a South American leaf fish, *Polycentrus schomburgkii*, with an account of recurring pseudofemale behavior. *Amer. Midl. Nat.* 78, 215-234.

BATEMAN, A.J. (1948) Intrasexual selection in *Drosophila*. *Heredity* 2, 349-368.

BEEBEE, T.J.C. (1981a) Habitats of the British amphibians (4): agricultural lowlands and a general discussion of requirements. *Biol. Conserv.* 21, 127-139.

BEEBEE, T.J.C. (1981b) Belly colour and foot-webbing in newts of the genus *Triturus*. *Brit. J. Herpetol.* 6, 59-61.

BELL, G. (1973) The life of the smooth newt, *Triturus vulgaris* (Linnaeus). PhD. Dissertation, University of Oxford.

BELL, G. (1977) The life of the smooth newt (*Triturus vulgaris*) after metamorphosis. *Ecol. Monogr.* 47, 279-299.

BELL, G. & LAWTON, J.H. (1975) The ecology of the eggs and larvae of the smooth newt (*Triturus vulgaris* (Linn.)). *J. Anim. Ecol.* 44, 393-423.

BELLIS, E.D. (1968) Summer movement of red-spotted newts in a small pond. *J. Herpetol.* 1, 86-91.

BENNETT, A.F. (1980) Activity metabolism of the lower vertebrates.

Ann. Rev. Physiol. 40, 447-469.

BENNETT, A.F. (1980) The metabolic foundations of vertebrate behavior.

BioScience, 30, 452-456.

BENSON, D.G. (1964) The histochemistry of the cloacal glands of the newt.

Am. Zool. 4, 408.

BIRKHEAD, T.R. & CLARKSON, K. (1980) Mate selection and precopulatory

guarding in *Gammarus pulex*. *Z. Tierpsychol.* 52, 365-380.

BOISSEAU, C. & JOLY, J. (1975) Transport and survival of spermatozoa in

female Amphibia. In E.S.E. Hafez & C.G. Thibault (eds). *The Biology of*

Spermatozoa. pp. 94-104. Karger, Basel.

BORGIA, G. (1979) Sexual selection and the evolution of mating systems.

In M.S. Blum & N.A. Blum (eds). *Sexual Selection and Reproductive*

Competition in Insects. pp. 19-80. Academic Press, London.

BRANDON, R.A., LABANICK, G.M. & HUHEEY, J.E. (1979) Relative palatability,

defensive behaviour and mimetic relationships of red salamanders

(*Pseudotriton ruber*), mud salamanders (*Pseudotriton montanus*) and red

efts (*Notophthalmus viridescens*). *Herpetologica*. 35, 289-303.

BUCHER, T.L., RYAN, M.J. & BARTHOLOMEW, G.A. (1982) Oxygen consumption

during resting, calling and nest building in the frog *Physalaemus*

pustulosus. *Physiol. Zool.* 55, 10-22.

BURLEY, N. (1981) Mate choice by multiple criteria in a monogamous species.

Am. Nat. 117, 515-528.

BURTON, T.M. (1977) Population estimates, feeding habits and nutrient and energy relationships of *Notophthalmus v. viridescens* in Mirror Lake, New Hampshire. *Copeia*. 1977, 139-143.

CADE, W. (1980) Alternative male reproductive strategies. *Fla. Ent.* 63, 30-45.

CANE, V.R. (1978) On fitting low-order Markov chains to behaviour sequences. *Anim. Behav.* 26, 332-338.

CLOUDSLEY-THOMPSON, J.L. (1976) *Evolutionary Trends in the Mating of Arthropoda*. Meadow field, Shildon.

CONANT, R. (1975) *A Field Guide to Reptiles and Amphibians of Eastern and Central North America*. Houghton Mifflin, Boston.

CONSTANTZ, G.D. (1975) Behavioral ecology of mating in the male gila top minnow, *Poeciliopsis occidentalis* (Cyprinodontiformes: Poeciliidae). *Ecology*. 56, 966-973.

COOKE, A.S. & FRAZER, J.F.D. (1976) Characteristics of newt breeding sites. *J. Zool.* 178, 223-236.

COX, C.R. & LE BOEUF, B.J. (1977) Female incitation of male competition: a mechanism in sexual selection. *Am. Nat.* 111, 317-335.

CREWS, D. (1980) Studies in squamate sexuality. *BioScience*. 30, 835-838.

CRIM, J.W. (1975) Prolactin-induced modification of visual pigments in the eastern red-spotted newt, *Notophthalmus viridescens*. *Gen. Comp. Endocrinol.* 26, 233-242.

CUPP, P.V. (1980) Territoriality in the green salamander, *Aneides aeneus*. *Copeia*. 1980, 463-468.

DARWIN, C. (1871) *The Descent of Man, and Selection in Relation to Sex*. John Murray, London.

DAVIES, N.B. (1982) Alternative strategies and competition for scarce resources. In King's College Sociobiology Group (eds). *Current Problems in Sociobiology*. pp. 363-380. Cambridge University Press, Cambridge.

DAVIES, N.B. & HALLIDAY, T.R. (1977) Optimal mate selection in the toad *Bufo bufo*. *Nature*. 269, 56-58.

DAWKINS, R. (1980) Good strategy or evolutionarily stable strategy? In G.W. Barlow & J. Silverberg (eds). *Sociobiology: Beyond Nature/Nurture?* pp. 331-367. Westview Press, Colorado.

DAWKINS, R. & KREBS, J.R. (1979) Arms races between and within species. *Proc. Roy. Soc. Lond., Ser. B.* 205, 489-511.

DE BOER, B.A. (1981) Influence of population density on the territorial, courting and spawning behaviour of male *Chromis cyanea* (Pomacentridae). *Behaviour*, 77, 99-120.

- DEMIAN, J.J. & TAYLOR, D.H. (1977) Photoreception and locomotor rhythm entrainment by the pineal body of the newt, *Notophthalmus viridescens* (Amphibia, Urodela, Salamandridae). *J. Herpetol.* 11, 131-139.
- DENT, J.N. (1970) The ultrastructure of the spermatheca in the red-spotted newt. *J. Morphol.* 132, 397-424.
- DEWSBURY, D.A. (1982) Ejaculate cost and male choice. *Am. Nat.* 119, 601-610.
- DOLMEN, D. (1976) Diel rhythm of *Triturus vulgaris*. *Norw. J. Zool.* 24, 234.
- DOLMEN, D. (1981) Local migration, rheotaxis and philopatry by *Triturus vulgaris* within a locality in central Norway. *Brit. J. Herpetol.* 6, 151-158.
- DOMINEY, W. (1980) Female mimicry in male bluegill sunfish - a genetic polymorphism? *Nature.* 284, 546-548.
- DOUGLAS, M.E. (1979) Migration and sexual selection in *Ambystoma jeffersonianum*. *Can. J. Zool.* 57, 2303-2310.
- DOWNHOWER, J.F. & ARMITAGE, K.B. (1971) The yellow-bellied marmot and the evolution of polygamy. *Am. Nat.* 105, 355-370.
- DOWNHOWER, J.F. & BROWN, L. (1981) The timing of reproduction and its behavioural consequences for mottled sculpins, *Cottus bairdi*. In R.D. Alexander & D.W. Tinkle (eds). *Natural Selection and Social Behaviour*. pp. 78-95. Blackwell, Oxford.

DUGAN, B. (1980) The social structure, communication and mating behavior of the green iguana (*Iguana iguana*). Ph.D. Dissertation, University of Knoxville.

DUNBAR, R.I.M. (1982) Intraspecific variations in mating strategy. In P.P.G. Bateson & P.H. Klopfer (eds). *Perspectives in Ethology, Volume 5*. pp. 385-431. Plenum, New York.

EDDY, F.B. & MCDONALD, P. (1978) Aquatic respiration of the crested newt *Triturus cristatus*. *Comp. Biochem. Physiol.* 59A, 85-88.

ELKAN, E. & COOPER, J.E. (1980) Skin biology of reptiles and amphibians. *Proc. Roy. Soc. Edinburgh.* 79B, 115-125.

EMLEN, S.T. & ORING, L.W. (1977) Ecology, sexual selection and the evolution of mating systems. *Science.* 197, 215-223.

ENSOR, D.M. (1978) *Comparative Endocrinology of Prolactin*. Chapman and Hall, London.

EVANS, L.T. (1960) Experiments relating to courtship of the newt *Diemyctylus viridescens*. *Anat. Rec.* 137, 353-354.

FARR, J.A. (1976) Social facilitation of male sexual behavior, intrasexual competition and sexual selection in the guppy, *Poecilia reticulata*. *Evolution.* 30, 707-717.

FARR, J.A. (1980) The effects of sexual experience and female receptivity on courtship-rape decisions in male guppies, *Poecilia reticulata* (Pisces: Poeciliidae). *Anim. Behav.* 28, 1195-1201.

GAGE, S.H. (1891) Life-history of the vermilion-spotted newt (*Diemyctylus viridescens* Raf.). *Am. Nat.* 25, 1084-1110.

GARTON, J.S. (1972) Courtship of the small-mouthed salamander, *Ambystoma texanum*, in southern Illinois. *Herpetologica.* 28, 41-45.

GATES, J.E. & THOMPSON, E.L. (1982) Small pool habitat selection by red-spotted newts in western Maryland. *J. Herpetol.* 16, 7-15.

GAUSS, G.H. (1961) Ein beitrag zur Kenntniss des Balzverhaltens einheimischer Molche. *Z. Tierpsychol.* 18, 60-66.

GERHARDT, H.C. (1981) Mating call recognition in the barking tree frog (*Hyla gratiosa*): responses to synthetic calls and comparisons with the green tree frog (*Hyla cinerea*). *J. Comp. Physiol.* 144, 17-25.

GILL, D.E. (1978a) The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). *Ecol. Monogr.* 48, 145-166.

GILL, D.E. (1978b) Effective population size and interdemic migration rates in a metapopulation of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). *Evolution.* 32, 839-849.

GILL, D.E. (1979) Density dependence and homing behavior in the red-spotted newts, *Notophthalmus viridescens* (Rafinesque). *Ecology.* 60, 800-813.

- GILL, D.E. & BERVEN, K.A. (In press) The environmental component of evolutionary biology. In C.A. King & P. Dawson (eds). *Population Biology: Retrospect and Prospect*. Columbia University Press, New York.
- GOIN, C.J., GOIN, O.B. & ZUG, G.R. (1978) *Introduction to Herpetology*. Freeman, San Francisco.
- GROSS, M.R. & CHARNOV, E.L. (1980) Alternative male life-histories in bluegill sunfish. *Proc. Nat. Acad. Sci., U.S.A.* 77, 6937-6940.
- GWYNNE, D.T. (1981) Sexual difference theory: Mormon crickets show role reversal in mate choice. *Science*. 213, 779-780.
- HAGSTROM, T. (1971) Stora vattensalamandern i Vastsverige - en predator pa sin mindre slakting. *Fauna och Flora*. 66, 71-72.
- HAGSTROM, T. (1973) Identification of newt specimens (Urodela, *Triturus*) by recording the belly pattern and a description of photographic equipment for such registrations. *Brit. J. Herpetol.* 4, 321-326.
- HAGSTROM, T. (1979) Population ecology of *Triturus cristatus* and *T. vulgaris* (Urodela) in S.W. Sweden. *Holarctic Ecol.* 2, 108-114.
- HAGSTROM, T. (1980a) Egg production of newts (*Triturus vulgaris* and *T. cristatus*) in southwestern Sweden. *ASRA Journal*. 1, 1-8.
- HAGSTROM, T. (1980b) Growth of newts (*Triturus cristatus* and *Triturus vulgaris*) at various ages. *Salamandra*. 16, 248-251.

HALLIDAY, T.R. (1972) A study of the behavior of newts. Ph.D. Dissertation, University of Oxford.

HALLIDAY, T.R. (1974) Sexual behavior of the smooth newt, *Triturus vulgaris* (Urodela, Salamandridae). *J. Herpetol.* 8, 277-292.

HALLIDAY, T.R. (1975a) On the biological significance of certain morphological characters in males of the smooth newt, *Triturus vulgaris* and of the palmate newt, *Triturus helveticus* (Urodela: Salamandridae). *Zool. J. Linn. Soc.* 56, 291-300.

HALLIDAY, T.R. (1975b) An observational and experimental study of sexual behaviour in the smooth newt, *Triturus vulgaris* (Amphibia, Salamandridae). *Anim. Behav.* 23, 291-322.

HALLIDAY, T.R. (1976) The libidinous newt. An analysis of variations in the sexual behaviour of the male smooth newt, *Triturus vulgaris*. *Anim. Behav.* 24, 398-414.

HALLIDAY, T.R. (1977a) The courtship of European newts. An evolutionary perspective. In D.H. Taylor & S.I. Guttman (eds). *The Reproductive Biology of Amphibians*. pp. 185-232. Plenum, New York.

HALLIDAY, T.R. (1977b) The effect of experimental manipulation of breathing on the sexual behaviour of the smooth newt, *Triturus vulgaris*. *Anim. Behav.* 25, 39-45.

HALLIDAY, T.R. (1978) Sexual selection and mate choice. In J.R. Krebs & N.B. Davies (eds). *Behavioural Ecology*. pp. 180-213. Blackwell, Oxford.

- HALLIDAY, T.R. (1980) Motivational systems and interactions between activities. In F.M. Toates & T.R. Halliday (eds). *Analysis of Motivational Systems*. pp. 205-220. Academic Press, London.
- HALLIDAY, T.R. (1983) The study of mate choice. In P.P.G. Bateson (ed). *Mate Choice*. pp. 3-32. Cambridge University Press, Cambridge.
- HALLIDAY, T.R. & HOUSTON, A. (1978) The newt as an honest salesman. *Anim. Behav.* 26, 1273-1274.
- HALLIDAY, T.R. & JOLY, P. (1981) The functional significance of foot-webbing in European newts (*Triturus*). *Brit. J. Herpetol.* 6, 131-132.
- HALLIDAY, T.R. & SWEATMAN, H.P.A. (1976) To breathe or not to breathe; the newt's problem. *Anim. Behav.* 24, 551-561.
- HALLIDAY, T.R. & VERRELL, P.A. (1983) Sperm competition in amphibians. In R.L. Smith (ed). *Sperm Competition and the Evolution of Animal Mating Systems*. Academic Press, London.
- HALLIDAY, T.R. & WORSNOP, A. (1977) Correlation between activity and breathing rate in the smooth newt, *Triturus vulgaris* (Amphibia, Urodela, Salamandridae). *J. Herpetol.* 11, 243-246.
- HAMILTON, W.D. (1971) Geometry for the selfish herd. *J. Theor. Biol.* 31, 295-311.
- HARDY, L.M. & RAYMOND, L.R. (1980) The breeding migration of the mole salamander, *Ambystoma talpoideum*, in Louisiana. *J. Herpetol.* 14, 327-335.

- HARRIS, R.N. (1981) Intrapond homing behavior in *Notophthalmus viridescens*. *J. Herpetol.* 15, 355-356.
- HARRISON, J.D., GITTINS, S.P. & SLATER, F.M. (1983) The breeding migrations of smooth and palmate newts (*Triturus vulgaris* and *T. helveticus*) at a pond in mid Wales. *J. Zool.* 199, 249-258.
- HEALY, W.R. (1973) Life history variation and the growth of juvenile *Notophthalmus viridescens* from Massachusetts. *Copeia* 1973, 641-647.
- HEALY, W.R. (1974) Sex ratio variation in samples of adult *Notophthalmus viridescens*. *Amer. Midl. Nat.* 92, 492-495.
- HEALY, W.R. (1975) Breeding and post-larval migrations of the red-spotted newt, *Notophthalmus viridescens*, in Massachusetts. *Ecology*. 56, 673-680.
- HEDGECOCK, D. (1978) Population subdivision and genetic divergence in the red bellied newt, *Taricha rivularis*. *Evolution*. 32, 271-286.
- HEMELAAR, A.S.M. & van GELDER, J.J. (1980) Annual growth rings in phalanges of *Bufo bufo* (Anura, Amphibia) from the Netherlands and their use for age determination. *Neth. J. Zool.* 30, 129-135.
- HERSHEY, J.L. & FORESTER, D.C. (1980) Sensory orietation in *Notophthalmus v. viridescens* (Amphidia: Salamandridae). *Can. J. Zool.* 58, 266-276.
- HILTON, W.A. (1902) A structural feature connected with the mating of *Diemyctylus viridescens*. *Am. Nat.* 34, 643-651.

HINDE, R.A. (1970) *Animal Behaviour*. McGraw-Hill, New York.

HOUSTON, A.I., HALLIDAY, T.R. & MCFARLAND, D.J. (1977) Towards a model of the courtship of the smooth newt, *Triturus vulgaris*, with special emphasis on problems of observability in the simulation of behaviour. *Med. Biol. Engin.* 15, 49-61.

HUMPHRIES, A.A. (1955) Observations on the mating behavior of normal and pituitary-implanted *Triturus viridescens*. *Physiol. Zool.* 28, 73-79.

HURLBERT, S.H. (1969) The breeding migrations and interhabitat wandering of the vermilion-spotted newt, *Notophthalmus viridescens* (Rafinesque). *Ecol. Monogr.* 39, 465-488.

HUSTING, E.L. (1965) Survival and breeding structure in a population of *Ambystoma maculatum*. *Copeia* 1965, 352-362.

JACKSON, R.R. (1982) The behavior of communicating in jumping spiders (Salticidae). In P.N. Witt & J.S. Rovner (eds). *Spider Communication: Mechanisms and Ecological Significance*. pp. 213-247. Princeton University Press, Princeton.

JANETOS, A.C. (1980) Strategies of female mate choice: a theoretical analysis. *Behav. Ecol. Sociobiol.* 7, 107-112.

JORDAN, E.O. (1891) The spermatophores of *Diemyctylus*. *J. Morphol.* 5, 263-270.

- KAPLAN, R.H. & SALTHER, S.N. (1979) The allometry of reproduction: an empirical view in salamanders. *Am. Nat.* 113, 671-689.
- KNOWLTON, N. (1983) Constraints imposed by selection on females. In R.L. Smith (ed). *Sperm Competition and the Evolution of Animal Mating Systems*. Academic Press, London.
- KUMPF, K.F. & YEATON, S.C. (1932) Observations on the courtship behavior of *Ambystoma jeffersonianum*. *Amer. Mus. Novitates*. 546, 1-7.
- LANTZ, L.A. (1947) Hybrids between *Triturus cristatus* Laur, and *Triturus marmoratus* Latr. *Proc. Zool. Soc. Lond.* 117, 247-258.
- LEHNER, P.N. (1979) *Handbook of Ethological Methods*. Garland STPM Press, New York.
- LLOYD, J.E. (1979) Sexual selection in luminescent beetles. In M.S. Blum & N.A. Blum (eds). *Sexual Selection and Reproductive Competition in Insects*. pp. 293-342. Academic Press, London.
- LOFTS, B. (1974) Reproduction. In B. Lofts (ed). *Physiology of the Amphibia, Volume 2*. pp. 107-218. Academic Press, London.
- LOTT, D.F. (1981) Sexual behavior and intersexual strategies in American bison. *Z. Tierpsychol.* 56, 97-114.
- LOW, B. (1978) Environmental uncertainty and the parental strategies of marsupials and placentals. *Am. Nat.* 112, 197-213.

- MACNAMARA, M.C. (1977) Food habits of terrestrial adult migrants and immature red eft of the red-spotted newt *Notophthalmus viridescens*. *Herpetologica*. 33, 127-132.
- MADISON, D.M. (1977) Chemical communication in amphibians and reptiles. In D. Muller-Schwarze & M.M. Mozell (eds). *Chemical Signals in Vertebrates*. pp. 135-168. Plenum, New York.
- MAYNARD SMITH, J. (1978) *The Evolution of Sex*. Cambridge University Press, Cambridge.
- MAYNARD SMITH, J. (1982) *Evolution and the Theory of Games*. Cambridge University Press, Cambridge.
- MCFARLAND, D.J. (1977) Decision making in animals. *Nature*. 269, 15-21.
- MORRIS, D. (1952) Homosexuality in the ten-spined stickleback. *Behaviour*. 4, 233-261.
- MORRIS, D. (1955) The causation of pseudofemale and pseudomale behaviour. *Behaviour*. 8, 46-56.
- MORRIS, D. (1956) The function and causation of courtship ceremonies in animals. In Fondation Singer-Polignac: *Colloque Internationale sur l'Instinct*. pp. 261-286. Paris.
- NAKATSURU, K. & KRAMER, D.L. (1982) Is sperm cheap? Limited male fertility and female choice in the lemon tetra (Pisces, Characidae). *Science*. 216, 753-755.

- NAYLOR, B.G. (1980) Radiation of the Amphibia Caudata: are we looking too far into the past? *Evol. Theory* 5, 119-126.
- NIE, N.H., HULL, C.H., JENKINS, J.G., STEINBRENNER, K. & BENT, D.H. (1975) *Statistical Package for the Social Sciences*. McGraw-Hill, New York.
- NOBLE, G.K. (1931) *The Biology of the Amphibia*. McGraw-Hill, New York.
- O'DONALD, P. (1980) *Genetic Models of Sexual Selection*. Cambridge University Press, Cambridge.
- ORGAN, J.A. (1958) Courtship and spermatophore of *Plethodon jordani metcalfi*. *Copeia* 1958, 251-259.
- ORGAN, J.A. (1960) Studies on the life-history of the salamander *Plethodon welleri*. *Copeia* 1960, 287-297.
- ORGAN, J.A. (1961) Studies of the local distribution, life history and population dynamics of the salamander genus *Desmognathus* in Virginia. *Ecol. Monogr.* 31, 189-200.
- ORGAN, J.A. & ORGAN, D.J. (1968) Courtship behavior of the red salamander, *Pseudotriton ruber*. *Copeia* 1968, 217-223.
- OTTE, D. (1979) Historical development of sexual selection theory. In M.S. Blum & N.A. Blum (eds). *Sexual Selection and Reproductive Competition in Insects*. pp. 1-18. Academic Press, London.

- PARKER, G.A. (1970) Sperm competition and its evolutionary consequences in the insects. *Biol. Rev.* 45, 525-567.
- PARKER, G.A. (1974) Courtship persistence and female-guarding as male time investment strategies. *Behaviour.* 48, 157-184.
- PARKER, G.A. (1979) Sexual selection and sexual conflict. In M.S. Blum & N.A. Blum (eds). *Sexual Selection and Reproductive Competition in Insects.* pp. 123-166. Academic Press, London.
- PARKER, G.A. (1983) Sperm competition and the evolution of animal mating strategies. In R.L. Smith (ed). *Sperm Competition and the Evolution of Animal Mating Systems.* Academic Press, London.
- PARKER, G.A., BAKER, R.R. & SMITH, V.G.F. (1972) The origin and evolution of gamete dimorphism and the male-female phenomenon. *J. Theor. Biol.* 36, 529-553.
- PETRANKA, J.W. & PHILLIPPI, A. (1979) Massive diurnal activity in non-migrating red eft of *Notophthalmus v. viridescens*. *Trans. Kentucky Acad. Sci.* 40, 96-97.
- PIKE, N. (1886) Some notes on the life-history of the common-newt. *Am. Nat.* 20, 17-25.
- PITKIN, R.B. & TILLEY, S.G. (1982) An unusual aggregation of adult *Notophthalmus viridescens*. *Copeia* 1982, 185-186.
- POPE, P.H. (1924) The life history of the common newt (*Notophthalmus viridescens*), together with observations on the sense of smell. *Carnegie Mus. Ann.* 15, 305-368.

PRECHTL, von H.F.R. (1951) Zur Paarungsbiologie einiger Molcharten.

Z. Tierpsychol. 8, 337-348.

PREMO, D.B. (1982) Some aspects of the ecology of the newt *Notophthalmus viridescens* Rafinesque in northern Michigan. *Jack-Pine Warbler.* 60, 119-120.

PUTNAM, R.W. (1979) The basis for differences in lactic acid content after activity in different species of anuran amphibians. *Physiol. Zool.* 52, 509-519.

REESE, A.M. (1917) The reactions of the crimson-spotted newt, *Diemystylus viridescens*, to light. *Anat. Rec.* 11, 521-522.

RIDLEY, M. & THOMPSON, D.J. (1979) Size and mating in *Asellus aquaticus* (Crustacea: Isopoda). *Z. Tierpsychol.* 51, 380-397.

RITTER, W.E. (1897) The life history and habits of the Pacific coast newt (*Diemystylus torosus* Esch.). *Proc. California Acad. Sci.* 3rd Ser. Zool. 1, 73-114.

ROBERTSON, H.M. (1982) Female courtship summation in *Drosophila melanogaster* *Anim. Behav.* 30, 1105-1117.

ROGOFF, J.L. (1927) The hedonic glands of *Triturus viridescens*: a structural and functional study. *Anat. Rec.* 34, 132-133.

ROHWER, S., FRETWELL, S.D. & NILES, D.M. (1980) Delayed maturation in passerine plumages and the deceptive acquisition of resources *Am. Nat.* 115, 400-437.

- ROSS, P. & CREWS, D. (1978) Stimuli influencing mating behavior in the garter snake, *Thamnophis radix*. *Behav. Ecol. Sociobiol.* 4, 133-142.
- ROWLAND, W.J. (1979) Stealing fertilizations in the fourspine stickleback, *Apeltes quadracus*. *Am. Nat.* 114, 602-604.
- RUBENSTEIN, D.I. (1980) On the evolution of alternative mating strategies. In J.E.R. Staddon (ed). *Limits to Action*. pp. 65-100. Academic Press, London.
- RUTOWSKI, R.L. (1982) Epigamic selection by males as evidenced by courtship partner preferences in the checkered white butterfly (*Pieris protodice*). *Anim. Behav.* 30, 108-112.
- SALTHER, S.N. (1967) Courtship patterns and the phylogeny of the urodeles. *Copeia* 1967, 100-117.
- SEVER, D.M. (1981) Cloacal anatomy of male salamanders in the families Ambystomatidae, Salamandridae and Plethodontidae. *Herpetologica*. 37, 142-155.
- SIEGEL, S. (1956) *Nonparametric statistics for the Behavioural Sciences*. McGraw-Hill, New York.
- SINGHAS, C.A. & DENT, J.N. (1975) Hormonal control of the tail fin and of the nuptial pads in the male red-spotted newt. *Gen. Comp. Endocrinol.* 26, 382-393.

- SMITH, M. (1951) *The British Amphibians and Reptiles*. Collins, London.
- SMITH, R.E. (1941) Mating behavior in *Triturus torosus* and related newts. *Copeia* 1941, 255-262.
- SPALLANZANI, L. (1780) *Dissertazioni di Fisica Animale e Vegetabile*. Moderna, Italy.
- SPOTILA, J.R. & BEUMER, R.J. (1970) The breeding habits of the ringed salamander, *Ambystoma annulatum* (Cope), in northwestern Arkansas. *Amer. Midl. Nat.* 84, 77-89.
- SPURWAY, H. & HALDANE, J.B.S. (1953) The comparative ethology of breathing. I. Breathing in newts, with a general survey. *Behaviour*. 6, 8-34.
- STEWART, J.W. (1969) *The Tailed Amphibians of Europe*. David and Charles, Newton Abbot.
- Storez, R.A. (1969) Observations on the courtship of *Ambystoma laterale*. *J. Herpetol.* 3, 87-95.
- THORNHILL, R. (1979) Adaptive female-mimicking behavior in a scorpion fly. *Science*. 205, 412-414.
- THORNHILL, R. (1980a) Competitive, charming males and choosy females: was Darwin correct? *Fla. Ent.* 63, 5-30.
- THORNHILL, R. (1980b) Rape in *Panorpa* scorpionflies and a general rape hypothesis. *Anim. Behav.* 28, 52-59.

- THORNHILL, R. (1981) *Panorpa* (Mecoptera: Panorpidae) scorpionflies: systems for understanding resource-defense polygyny and alternative male reproductive efforts. *Ann. Rev. Ecol. Syst.* 12, 355-386.
- TINBERGEN, N. (1953) *Social Behaviour in Animals*. Methuen, London.
- TINBERGEN, N. (1963) On aims and methods of ethology. *Z. Tierpsychol.* 20, 410-433.
- TRIVERS, R.L. (1972) Parental investment and sexual selection. In B. Campbell (ed). *Sexual Selection and the Descent of Man, 1871-1971*. pp. 136-179. Aldine, Chicago.
- TRIVERS, R.L. (1976) Sexual selection and resource-accruing abilities in *Anolis garmani*. *Evolution*. 30, 253-269.
- TSUTSUI, Y. (1931) Notes on the behaviour of the common Japanese newt *Diemyctylus pyrrhogaster* Boie. I. Breeding habit. *Mem. Coll. Sci. Kyoto Imp. Univ., Ser. B.* 7, 159-178.
- van den ASSEM, J. (1967) Territory in the three-spined stickleback. *Behaviour. Suppl.* 16, 1-164.
- van GELDER, J.J. (1979) Differences in the sexual behaviour of the smooth newt *Triturus vulgaris* and the palmate newt *Triturus helveticus*. *Bull. Soc. Zool. France.* 102, 23-26.
- VERRELL, P.A. (1982a) Newts can be colourful too. *BioScience.* 32, 244.

- VERRELL, P.A. (1982b) A note on the maintenance of the red-spotted newt in captivity. *BHS Bull.* 5, 28.
- VERRELL, P.A. (1982c) The sexual behaviour of the red-spotted newt, *Notophthalmus viridescens* (Amphibia: Urodela: Salamandridae). *Anim. Behav.* 30, 1224-1236.
- VERRELL, P.A. (1982d) Male newts prefer large females as mates. *Anim. Behav.* 30, 1254-1255.
- VERRELL, P.A. (In press) A note on the breeding of the red-spotted newt in captivity. *BHS Bull.*
- WADE, M.J. & ARNOLD, S.J. (1980) The intensity of sexual selection, in relation to male sexual behaviour, female choice and sperm precedence. *Anim. Behav.* 28, 446-461.
- WAKE, D.B. & OZETI, N. (1969) Evolutionary relationships in the family Salamandridae. *Copeia* 1969, 124-137.
- WALKER, W.F. (1980) Sperm utilization strategies in non social insects. *Am. Nat.* 115, 780-799.
- WELLS, K.D. (1977) The social behaviour of anuran amphibians. *Anim. Behav.* 25, 666-693.
- WELLS, K.D. (1980) Spatial associations among individuals in a population of slimy salamanders (*Plethodon glutinosus*). *Herpetologica*. 36, 271-275.

WEYGOLDT, P. (1966) Spermatophore web formation in a pseudoscorpion. *Science*, 153, 1647-1649.

WIKLUND, C. (1982) Behavioural shift from courtship solicitation to mate avoidance in female ringlet butterflies (*Aphantopus hyperanthus*) after copulation. *Anim. Behav.* 30, 790-793.

WILLIAMS, G.C. (1975) *Sex and Evolution*. Princeton University Press, Princeton.

WILSON, E.O. (1975) *Sociobiology: The New Synthesis*. Belknap Press, Harvard.

WIRTZ, P. (1978) The behavior of the Mediterranean *Tripterygion* species (Pisces, Blennioidei). *Z. Tierpsychol.* 48, 142-174.

WOOD, J.T. & GOODWIN, O.K. (1954) Observations on the abundance, food and feeding behavior of *Notophthalmus viridescens* (Rafinesque) in Virginia. *J. Mitchell Soc.* 1954, 27-30.

ZELLER, E. (1880) Über die Befruchtung bei den Urodelen. *Z. Wissen. Zool.* 49, 583-601.

ZIMMER, J.A. & DENT, J.N. (1981) Hormonal regulation of nuptial pads and tail fins in the female red-spotted newt. *Gen. Comp. Endocrinol.* 44, 436-443.